

LATE TREMADOC GRAPTOLITES FROM WESTERN NEWFOUNDLAND

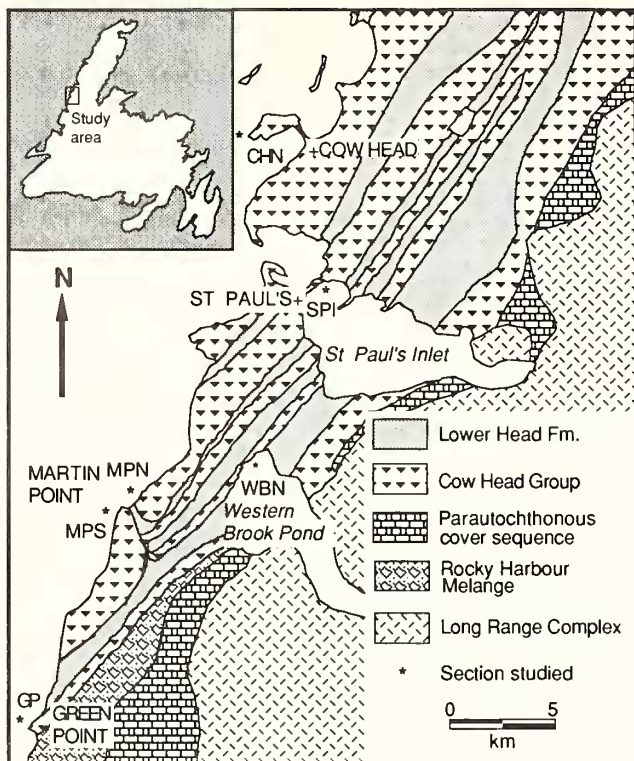
by S. HENRY WILLIAMS and ROBERT K. STEVENS

ABSTRACT. The Cow Head Group of western Newfoundland preserves a sequence of carbonate-rich sediments ranging from middle Cambrian to middle Ordovician. It yields a rich graptolite fauna both with flattened specimens in black shales and cherts, and three-dimensional and flattened material in nodular limestones which may be isolated from the rock by acid extraction. A continuous succession is present across the Tremadoc–Arenig boundary, containing a well represented graptolite assemblage which is here referred to the *A. victoriae* Zone. Late Tremadoc graptolite faunas have been documented from many localities around the world, but are commonly found in stratigraphically incomplete sequences and have only been known previously from non-isolated material. The Cow Head Group faunas comprise both flattened and isolated material, allowing detailed observation of proximal developments to be compared with overall rhabdosome forms. Several taxa possess overall forms, proximal structures and thecal styles somewhat similar to dichograptids and sigmagraptines found in the early Arenig, but they all possess a sicular bitheca; some have additional bithecae associated with the autothecae, and dichotomous branching is commonly far more variable. Because of these differences, all taxa described from this interval are considered to belong to the Anisograptidae, necessitating some generic reassignment and the erection of several new taxa. These include *Kiaerograptus undulatus* sp. nov., *K. magnus* sp. nov., *Paratennograptus isolatus* sp. nov., *Aorograptus* gen. nov., *Adelograptus altus* sp. nov. and *A. filiformis* sp. nov.

DURING the latter part of the Tremadoc Series, some of the planktonic graptolites (traditionally assigned to the Dendroidea) which were components of Bulman's (1954) Anisograptid Fauna, underwent significant evolutionary changes. These involved the loss of bithecae and sclerotized stolons and general simplification of stipe geometry. This Anisograptid Fauna gave way to the typical graptoloid-dominated Dichograptid Fauna by the earliest Arenig. The adaptive reasons for the changes are not fully understood; the loss of bithecae which are generally considered to have played a role in reproduction (e.g. Kozłowski 1949; Rickards 1977) is particularly puzzling. Fortey and Cooper (1986) have challenged the traditional high-level classification of the graptolites; they assign all nematophorous (planktonic or epiplanktonic) graptolites to the Graptoloidea, including the anisograptids such as *Rhabdinopora* (ex *Dictyonema* – see Erdtmann 1982). In their scheme, only forms which remained benthic throughout ontogeny are referred to the Dendroidea.

Cooper (1979b) reviewed the global distribution, zonation and correlation of Tremadoc graptolite assemblages. Late Tremadoc assemblages, which Cooper assigned to an Assemblage 4, are characterized by a large and diverse graptolite fauna including species formerly assigned to *Adelograptus*, *Bryograptus*, *Kiaerograptus*, *Tennograptus*, *Tetragraptus*, *Didymograptus* and *Clonograptus*. His following Assemblage 5 marks the base of the Arenig and is characterized by the appearance of *Tetragraptus approximatus*. Assemblage 4 faunas are perhaps best known from Australasia; other areas where they occur include China (southwest, Kiangsi), USSR (Kazakhstan, Taimyr), Europe (Oslo Region, Sweden and south-west Spain), and North America (Yukon, Texas, Quebec and western Newfoundland). Although many graptolitic units are therefore present through this interval, graptolites of late Tremadoc age are not commonly found well preserved, neither are they normally in sequence with stratigraphically older and younger, graptolite-bearing strata. In addition, evidence for a late Tremadoc age from other taxa is usually lacking, and little or no late Tremadoc isolated, three-dimensional material has been described to date.

Martin Point (Text-fig. 1) was the only locality in western Newfoundland discussed by Cooper



TEXT-FIG. 1. Geological map of the Cow Head region, western Newfoundland (after Williams and Stevens 1988, text-fig. 2).

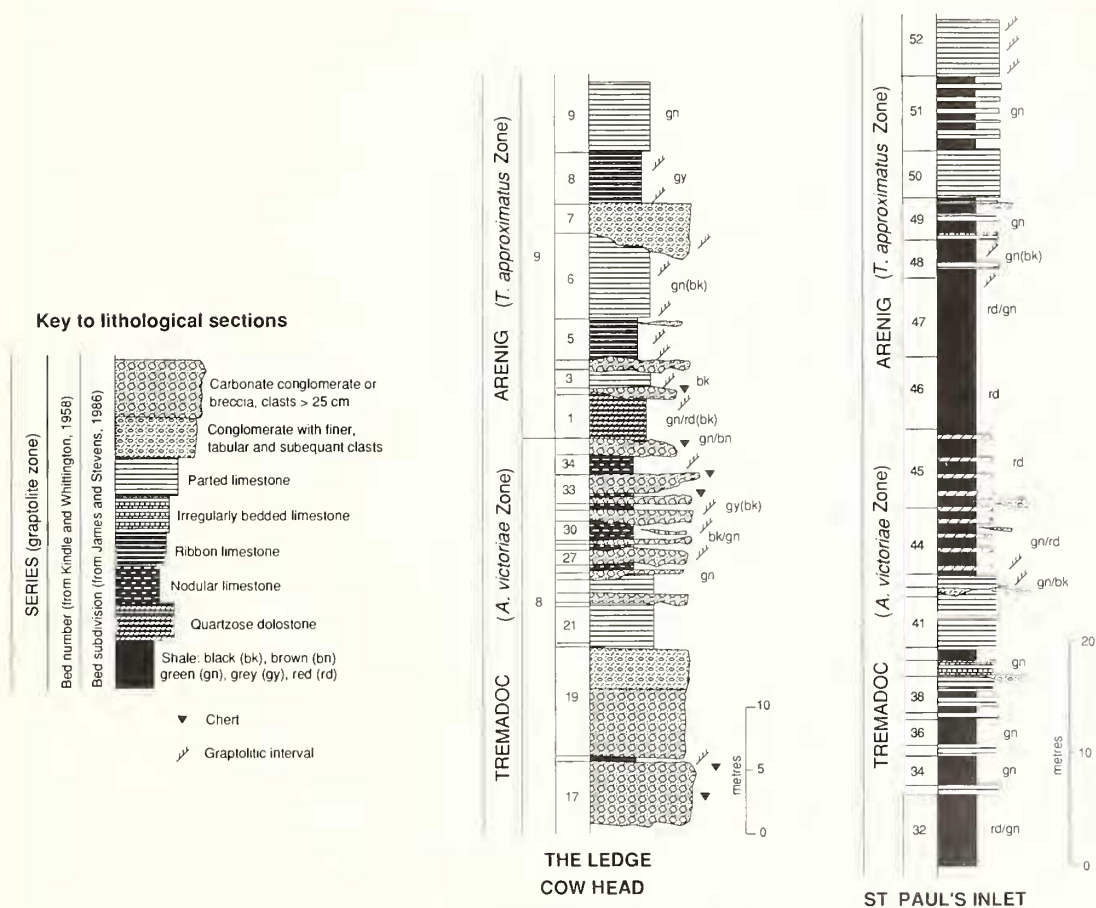
(1979*b*). His data were derived from Erdtmann (1971*a, b*) who in turn had relied on preliminary information from Kindle and Whittington (1958). Since that time, other sections yielding late Tremadoc graptolites have been described by James and Stevens (1986), and it is both on Martin Point and these additional sections that the present paper is based. The importance of early Ordovician graptolites from the Cow Head Group has recently been illustrated through the work of Williams and Stevens (1988*a*), who described the Arenig faunas. Rich assemblages of flattened material are found in structurally-simple stratigraphic sequences, and are occasionally associated with three-dimensional, isolatable material from nodular limestones at the same horizons. Not only is there a stratigraphically-continuous sequence of graptolites from the late Tremadoc through to the earliest Arenig *T. approximatus* Zone, but the graptolites are also associated with other fossil groups within the black shales and nodular limestones, including conodonts and trilobites.

GEOLOGICAL AND STRUCTURAL SETTING OF THE COW HEAD GROUP

During the late Cambrian and early Ordovician, western Newfoundland formed part of the low latitude Laurentian continental margin, facing the Iapetus Ocean to the south-west (Williams and Stevens 1974). This area now lies within the Humber tectonostratigraphic zone of the Appalachians (Williams 1978). Two distinct sedimentary sequences were deposited along the margin; on the shelf itself, a predominately carbonate sequence (James *et al.* 1989) formed in shallow, tropic seas, while on the continental slope and rise a coeval sequence of shales and turbidites, the Humber Arm Supergroup, was deposited. The shelf/continental rise has since been destroyed by subsequent tectonism, and its former location can only be surmised (Rodgers 1968). That part of the Humber Arm Supergroup on the Northern Peninsula characterized by limestone conglomerates, thin bedded

limestones, and shales is referred to as the Cow Head Group (Kindle and Whittington 1958; James and Stevens 1986).

The Humber Arm Supergroup, including the Cow Head Group, was transported westward during Llanvirn tectonism. It was pushed over the shelf sequence as part of a large allochthon, the Humber Arm Allochthon. Since the upper part of the allochthon contains large slabs of ophiolite-derived material and fragments of volcanic islands, the tectonism was probably the result of the abortive subduction of the Laurentian margin under Iapetus. Remarkably, the slices of allochthon containing the Cow Head Group escaped with little deformation during transport, although later (early Devonian?) imbrication resulted in some brittle-style deformation. The lack of pervasive alteration is demonstrated well by the conodont Colour Alteration Index (CAI), which reaches only 1.5 in the Cow Head region (Nowlan and Barnes 1987). As a result of these tectonic events and subsequent erosion, the Cow Head Group is now exposed in a series of thrust slices that span some 25 km across depositional strike (Text-fig. 2).



TEXT-FIG. 2. Lithological logs through the Cow Head Group for the Tremadoc–Arenig boundary interval at Cow Head and St Paul's Inlet, indicating graptolitic horizons (after James and Stevens, 1986).

Geology of the Cow Head Group

The following account is based largely on James and Stevens (1986), from whom additional details may be obtained. The Cow Head Group consists of up to 500 m of shales, hemipelagic limestones,

carbonate grainstones and limestone conglomerates. The detrital carbonates were deposited through the action of lime turbidites and limestone debris flows derived in part from lithified or semi-lithified sediments of the shelf edge and upper slope to the north-west. Most, but not all, clasts from any particular conglomerate yield fossils from a limited stratigraphic range and are approximately coeval with fossils from the overlying shales and limestones. This permits an unusually high degree of correlation between typical shelf faunas and those inhabiting deeper, open ocean environments, although care needs to be exercised in recognizing reworked faunal assemblages. The most common fossils in the limestone clasts are trilobites (see Kindle and Whittington, 1958), brachiopods (see Ross and James 1987) and conodonts (see Pohler *et al.* 1987) of the North American conodont province. The interbedded shales and limestones yield graptolites, conodonts of the North Atlantic province, inarticulate brachiopods and occasional trilobites, together with rare examples of other invertebrates and possible fish remains. The graptolite record extends from the middle Cambrian to the early middle Ordovician (late Arenig); details of the post-Tremadoc, early Ordovician graptolites are given by Williams and Stevens (1987, 1988a). A fuller account of previous investigations into graptolites from the Cow Head Group is also provided in the latter work. Other recent publications on the invertebrate faunas include accounts of the conodonts straddling the Cambrian–Ordovician boundary (Barnes 1988) and the Tremadoc–Arenig boundary (Stouge and Bagnoli 1988), and notes on the Radiolaria (Iams and Stevens, 1988; Stevens and Iams 1988). A monographic study of the Cambrian trilobite fauna has recently been completed by Ludvigsen *et al.* (1989).

Biostratigraphic correlation between the isolated sections through the Cow Head Group, based mainly on graptolites and trilobites, shows that several conglomerate horizons can be traced throughout the entire Cow Head area. Those conglomerates in the most north-easterly exposures are thickest and coarsest, and interpreted to have been deposited closest to source. The most proximal sections of Stearing Island and Lower Head are composed almost entirely of conglomerate with only narrow interbeds; one boulder at Lower Head is 200 m across (Kindle and Whittington, 1958). The distal sections such as that at Green Point are mainly shale and thin-bedded limestone; here the conglomerates are thin with only small clasts up to 20 cm diameter.

The proximal sections in the Cow Head Group were originally upslope from the more distal, and this may have controlled the distribution of graptolites to some extent. A noticeable feature of the distal section is the development of red, bioturbated shales in the late Tremadoc and Arenig, although at Cow Head itself the only heavily oxidized sediments present are found in a 3.3 m thick greenish dolostone interval at the Tremadoc–Arenig boundary. The overall colour change in Arenig shale interbeds, from dominantly green and black proximally to almost entirely red in the more distal sections, suggests an oxygen minimum upslope, with increased ventilation in deeper waters as found at the present time (see James and Stevens 1986). The ubiquitous red strata across the Tremadoc–Arenig boundary must, however, reflect important changes in the structure of at least the western reaches of the Iapetus Ocean, and may be of global significance (Stevens in prep.). It is possible that a stratified Cambrian ocean with anoxic bottom waters changed into a mixed ocean with oxygenated bottom waters during the Tremadoc, perhaps as a result of the glacial event postulated by Fortey and Morris (1982). Such a change, particularly if it occurred during the Tremadoc–Arenig boundary interval, may well have influenced the course of graptolite evolution in a similar fashion to the extinction and radiation event during the late Ordovician (Barnes and Williams 1990).

Stratigraphic nomenclature of the Cow Head Group

The earliest workers who studied the rocks of western Newfoundland, namely Richards, Billings and Logan (*in* Logan 1863), correlated the Cow Head strata with similar rocks in Quebec, particularly with those at Levis. Logan (1863) placed the Cow Head Group in his Division P. Schuchert and Dunbar (1934) concluded that the Cow Head was in part a tectonic breccia of middle Ordovician age. Kindle and Whittington (1958), following the lead given by Johnson (1941), recognized that the strata represented a sequence of sediments with an orderly stratigraphy and that

Figure 1 displays four stratigraphic columns representing different localities, showing the sequence of geological units and their lithological characteristics. The columns are labeled as follows:

- WESTERN BROOK POND (NORTH):** The column shows the Tremadoc zone (units 1-5) and the Arenig zone (units 8-19). The Tremadoc units are primarily green shale (gn) and red shale (rd). The Arenig units are primarily red shale (rd) and green shale (gn), with some green shale with red beds (gn/rd) and green shale with black beds (gn/bk). A note indicates "no exposure green shale in water" for the lower Tremadoc units.
- MARTIN POINT (NORTH):** The column shows the Tremadoc zone (units 1-12) and the Arenig zone (units 14-30). The Tremadoc units are primarily red shale (rd) and green shale (gn), with some green shale with black beds (gn/bk). The Arenig units are primarily red shale (rd) and green shale (gn), with some green shale with black beds (gn/bk) and green shale with green beds (gn/gy).
- MARTIN POINT (SOUTH):** The column shows the Tremadoc zone (units 1-41) and the Arenig zone (units 42-43). The Tremadoc units are primarily red shale (rd) and green shale (gn), with some green shale with black beds (gn/bk) and green shale with red beds (gn/rd). The Arenig units are primarily red shale (rd) and green shale (gn), with some green shale with black beds (gn/bk) and green shale with red beds (gn/rd).
- GREEN POINT:** The column shows the Tremadoc zone (units 1-36) and the Arenig zone (units 37-43). The Tremadoc units are primarily red shale (rd) and green shale (gn), with some green shale with black beds (gn/bk) and green shale with red beds (gn/rd). The Arenig units are primarily red shale (rd) and green shale (gn), with some green shale with black beds (gn/bk) and green shale with red beds (gn/rd).

Correlation with other sequences

Full discussion of correlation between graptolitic zonal schemes of the early Ordovician was given by Cooper (1979*b*). Since that time, additional sections have been studied; we therefore include an

SERIES	COW HEAD W. NFDL 1	VICTORIA AUSTRALIA 2	NEW ZEALAND 3	CANADIAN CORDILLERA 4	TEXAS 5	CENTRAL GREAT BRITAIN 6	OSLO NORWAY 7	HUNNEBERG SWEDEN 8	HUNJIANG CHINA 9
ARENIG	<i>P. fruticosus</i>	Be4 <i>T. fruti. (3 stipe)</i>						no fauna recorded	
		Be3 <i>T. fruti. (3 & 4)</i>							
	<i>T. akzharensis</i>	Be2 <i>T. fruticosus (4)</i>	<i>T. fruticosus</i>	<i>T. fruticosus</i>	<i>T. fruticosus</i>		D'ydimograptus Beds	<i>T. approximatus</i>	
		Be1 <i>T. fruticosus & T. approximatus</i>						<i>T. phyllo- graptoides</i>	no fauna recorded
TREMADOC	<i>T. approximatus</i>	La3 <i>T. approximatus</i>	<i>T. approximatus</i>	<i>T. approximatus</i>	<i>T. approximatus</i>	hiatus	hiatus	<i>U. planilimba</i>	
	<i>A. victoriae</i>	La2 <i>A. victoriae</i>	<i>Adelograptus</i>	<i>Adelograptus</i>	<i>C. flexilis - A. victoriae</i>			<i>P. antiquus</i>	<i>Adelograptus - Clonograptus</i>
	zones not yet defined	La1.5 <i>Psigraptus & Clonograptus</i>	no fauna recorded	no fauna recorded	<i>Anisograptus - Steuropgraptus</i>	<i>S. pusille</i>	Ceratopyge Beds	<i>E. armata</i>	
								<i>A. serratus</i>	<i>Psigraptus</i>
						<i>C. tenellus</i>		<i>A. tenellus</i>	<i>Anisograptus</i>
		La1 <i>D. scitulum & Anisograptus</i>				<i>D. l. flebelli- forme</i>	Dictyonema Beds	no fauna recorded	<i>R. parabola</i>

TEXT-FIG. 4. Correlation of the late Tremadoc-early Arenig graptolite zones of the Cow Head Group with other sequences (data based largely on: 1 - Williams and Stevens 1988a and this paper; 2 - VandenBerg 1981; 3 - Cooper 1979a; 4 - Lenz and Jackson 1986; 5 - Berry 1960; 6 - Stubblefield and Bulman 1929; 7 - Monsen 1925; 8 - Maletz and Erdtmann 1987; 9 - Wang and Erdtmann 1986).

updated correlation chart to include a selection of these (Text-fig. 4), although some (e.g. Hunneberg and Oslo) are currently under investigation and detailed biostratigraphic discussion is not yet possible. For the purpose of the present paper, we merely reiterate the precise correlation possible in continuously graptolitic successions across the Tremadoc-Arenig boundary interval, where a rapidly evolving graptoloid fauna, as found in the *A. victoriae* Zone in the Cow Head Group, becomes extinct and is then replaced by the somewhat low-diversity but distinctive dichograptid fauna of the *T. approximatus* Zone (see Williams and Stevens 1988a). Several anisograptid genera, including *Rhabdinopora*, surprisingly seem to have been unaffected by this evolutionary event, maintaining their relative abundance from the late Tremadoc through to the *T. akzharensis* Zone. These taxa are, however, rare in the succeeding *P. fruticosus* and later Arenig zones, where the fauna is dominated by dichograptids and sigmagraptines.

Justification for employing the chronostratigraphic series 'Tremadoc' and 'Arenig' is, however, more difficult owing to the incomplete nature of original British sections and the current state of flux regarding their definition (see Fortey 1988). Ongoing biostratigraphic studies within the Cow Head Group, particularly of the conodonts and trilobites (see Barnes *et al.* 1988; Stouge and Bagnoli 1988; Williams and Stevens 1988b), are permitting precise correlation between the various schemes at this level. These support the assumption made by most previous graptolite workers (e.g. Bulman 1970; Cooper 1979b) that the major faunal turnover documented at a level equivalent to the boundary between the *A. victoriae* and *T. approximatus* zones lie close to the traditionally accepted position of the Tremadoc-Arenig boundary.

TAXONOMIC PROBLEMS ASSOCIATED WITH LATE TREMADOC GRAPTOLITES

The earliest graptolites from the Cambrian were all benthic (see Rickards 1977); the first planktic graptolites evolved during the Cambrian–Ordovician boundary interval, including the ubiquitous and familiar group of *Rhabdinopora flabelliformis*. These Tremadoc anisograptids have traditionally been assigned to the Dendroidea, characterized by numerous, commonly irregular dichotomies, presence of bithecae, and a sclerotized stolon. Fortey and Cooper (1986) produced a revised high level, phylogenetic classification, in which they assigned all nematophorous (i.e. planktic and epiplanktic) graptolites to the Graptoloidea, restricting the Dendroidea to benthic genera. For the purpose of the present work, we accept this revised notion; consequently all taxa described herein are considered to be Graptoloidea.

Bulman (1970) referred all Tremadoc nematophorous graptolites to the Anisograptidea; these were subsequently split into four subfamilies, the Adelograptinae, Anisograptinae, Staurograptinae, and Rhabdinoporinae, although Fortey and Cooper (1986, p. 683) doubted that these groupings served any useful, phylogenetically-related purpose. Further studies utilizing isolated material such as the present one are required before any additional revision of high-level classification is possible; until that time we follow Fortey and Cooper (1986) in using an undivided family Anisograptidae.

Previous publications describing late Tremadoc graptolites have assigned them to both anisograptid and dichograptid taxa, for while some elements of the fauna (e.g. *Rhabdinopora*) are clearly identical to earlier Tremadoc taxa, others appear more similar in overall rhabdosome form to ‘typically’ Arenig dichograptids, commonly having only two to four stipes and relatively simple thecal style. These species have been variably assigned to anisograptid genera such as *Adelograptus* and *Kiaerograptus*, and to dichograptid genera including *Tetragraptus* and *Didymograptus* (e.g. Jackson 1974; Cooper and Stewart 1979). None of these previous studies had the opportunity of utilizing isolated, three-dimensional material to substantiate deductions made from flattened, non-isolated species. Most material described here from the Cow Head Group is flattened, but three nodular limestone horizons (at Martin Point South, Green Point and St Paul’s Inlet) have yielded three-dimensional graptolites that can be isolated from the rock using acetic acid. These generally lack fine detail of periderm structure owing to the rather coarse, granular nature of preservation, probably related to partial breakdown of the organic material during subsequent burial and tectonic deformation. A few specimens do, however, reveal some ultrastructure, including cortical bandages overlying the fusellar increments (Text-fig. 5). Most studies of periderm ultrastructure have been made on graptolites of middle Ordovician and Silurian age, Rickards *et al.* (1982) recording no studies at all on material from the Tremadoc. Our material is thus important in providing a comparison of structures described from later taxa, although the main value of isolated specimens from the Cow Head Group is in permitting observation of proximal development. This has allowed us to make the following conclusions:

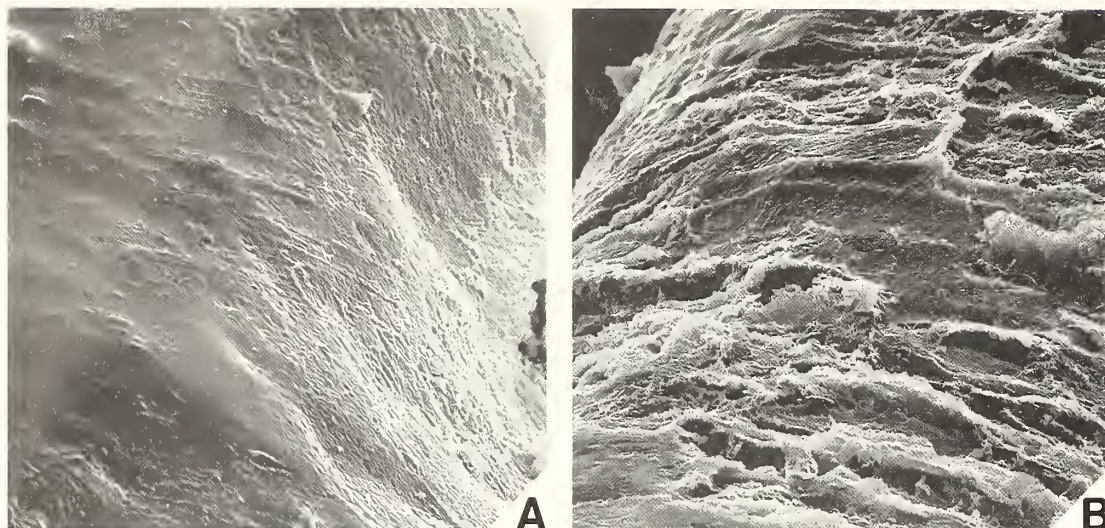
1. Whereas presence of bithecae associated with autothecae is variable, all taxa from this interval possess a sicular bitheca. A sicular bitheca has never been recorded from any Arenig dichograptid or sigmagraptine species, although it is apparently present in all earlier Tremadoc anisograptids (see Rickards 1975, 1977).

2. With the exception of the sicular bitheca, proximal development of several late Tremadoc species is almost indistinguishable from that of certain early Arenig dichograptid and sigmagraptine taxa described by Williams and Stevens (1988a).

3. Although overall rhabdosome form of a few taxa are similar to Arenig dichograptids and sigmagraptines, irregular occurrence of delayed dichotomies commonly results in extra stipes of variable number. This contrasts with the regular, fixed nature of branching in the Arenig taxa.

4. Genera such as *Rhabdinopora* and *Clonograptus* which are found earlier in the Tremadoc and continue through into the Arenig have distinctive proximal developments unlike those of the majority of the fauna, and bithecae throughout the rhabdosome.

We consider that the presence of a sicular bitheca and irregular dichotomous branching does not permit the assignment of any late Tremadoc graptolites to the Dichograptidae or Sigmagraptinae,



TEXT-FIG. 5. SEM micrographs showing details of ultrastructure on isolated metasicula of *Kiaerograptus bulmani* (Thomas, 1973), GSC 87446, SPI43 (complete specimen figured Pl. 3, fig. 12). A, cortical bandages, $\times 110$. B, fusellar increments, $\times 110$.

unless the traditionally accepted views of these high-level classifications is significantly modified. All taxa described herein are therefore assigned to existing or new anisograptid genera. It does, however, seem likely that several late Tremadoc genera give rise to Arenig forms through loss of bithecae and the fixing of dichotomous branching, perhaps suggesting a polyphyletic origin for the dichograptids and sigmagraptines. This will be the subject of a future study incorporating both Tremadoc and Arenig material, and is outside the scope of the present paper.

SYSTEMATIC PALAEOLOGY

Descriptive nomenclature employed conforms to that of Bulman (1970), Cooper and Fortey (1982) and Williams and Stevens (1988a). Particular note should be made of the term 'rutellum', introduced by Williams and Stevens (1988a, p. 20) to describe the 'lip' or 'spoon-shaped' process found at the sicular aperture of many Ordovician graptolites on the side of $th1^1$ (*cf.* the virgella, which is a spine). The acetate overlay technique described by Williams and Stevens (1988a, p. 23) was employed to assist in distinguishing species and in comparing isolated specimens with flattened material.

Line drawings were made whilst using a Wild M5A microscope with 'camera lucida' attachment. Light photographs of isolated and non-isolated material were taken with a Wild M400 photomicroscope, using fibre-optic light source and with slabs immersed in 95% ethanol. Scanning electron micrographs were taken using a Hitachi S570 with a 120 film back.

All figured specimens are housed in the collections of the Geological Survey of Canada, Ottawa (GSC). Specimen localities and horizons in the systematic section are referred to in abbreviated form; collected sections (see Text-fig. 1 and Williams and Stevens 1988a) are the 'Ledge' on the Cow Head Peninsula (CHN), St Paul's Inlet, North Tickle (SPI), Western Brook Pond, north section (WBN), Martin Point, north and south sections (MPN and MPS), and Green Point (GP). Numbered intervals refer to those used in Text-figures 2 and 3.

Order GRAPTOLOIDEA
Family ANISOGRAPTIDAE Bulman, 1960
Genus KIAEROGRAPTUS Spjeldnaes, 1963

Type species. *Didymograptus kiaeri* Monsen, 1925, pp. 172–175, pl. 2, figs 9, 10, 12–14, 16, pl. 4, figs 6–8. By original designation.

Diagnosis (revised). Rhabdosome horizontal or declined, with two primary stipes, one or both of which may dichotomise at the second thecal pair to produce three or four stipes. Autothecae simple or with sigmoidal curvature, prothecal folds occasionally present. Sicular with bitheca; other bithecae present in early forms, apparently absent in later taxa.

Remarks. The definition of *Kiaerograptus* was revised by Bulman (1970) and by Cooper and Stewart (1979); the description of *K. quasimodo* by Rushton (1981) and of taxa in the present study necessitate a broadening of the understanding to include rhabdosomes with more than two stipes as originally defined.

Further revision might permit restriction of the genus to include only taxa with sigmoidally curved thecae and prothecal folds, as found in *K. kiaeri*, *K. quasimodo*, and the two new species erected in the present study (*K. undulatus* and *K. magnus*). This morphological feature is, however, often difficult to recognize in flattened material, and apparent folding of the dorsal margin is sometimes a post-mortem effect related to diagenetic flattening.

All species included within *Kiaerograptus* from western Newfoundland have similar proximal development, but show some variation in thecal style; none, however, possesses any bithecae other than that of the sicular, and possibly at the dichotomies of first order stipes. Species from earlier in the Tremadoc, such as *K. kiaeri* and *K. quasimodo* have bithecae associated with autothecae throughout much of the rhabdosome, and a gradual reduction in bithecae would probably be documented if a continuous stratigraphic succession of taxa could be found.

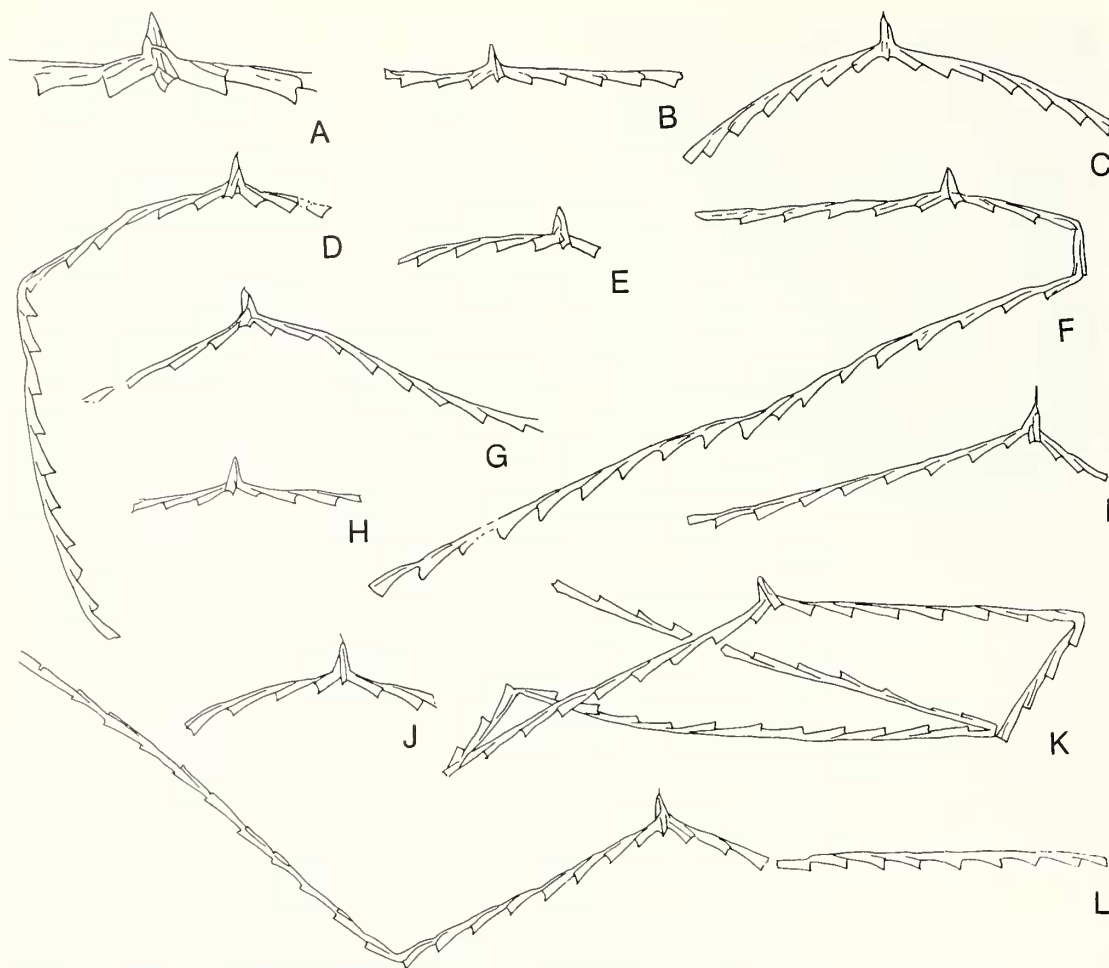
Kiaerograptus pritchardi (T. S. Hall, 1899)

Plate 1, fig. 1; Text-fig. 6A-L

- 1899 *Didymograptus pritchardi*, n. sp.; T. S. Hall, p. 167, pl. 17, figs 7 and 9; pl. 19, figs 8 and 10.
- 1938b *Didymograptus pritchardi* T. S. Hall; Harris and Thomas, pl. 1, fig. 13.
- 1960 *Didymograptus pritchardi* T. S. Hall; Thomas, pl. 1, fig. 14.
- ?1962 *Didymograptus temiramis* sp. nov.; Obut and Sobolevskaya, pp. 84–85, pl. 5, fig. 3.
- 1966 *Didymograptus pritchardi* T. S. Hall; Berry, pp. 429–430, pl. 45, fig. 1; pl. 46, fig. 1; pl. 47, figs 1 and 2.
- 1974 *Didymograptus*(?) *stelcki* n. sp.; Jackson, pp. 52–53, pl. 5, figs 5 and 7; text-fig. 1a, b.
- non 1974 *Kiaerograptus pritchardi* (T. S. Hall); Jackson, p. 51, pl. 5, fig. 3; text-fig. 2a, c, d (= *A.?* *filiformis* sp. nov.).
- 1979b *Kiaerograptus* cf. *pritchardi* (T. S. Hall); Cooper, fig. 5a.
- non 1982 *Kiaerograptus pritchardi* (T. S. Hall); Gutierrez-Marco, fig. 2f (= *K. taylori*).

Type specimen (designated Berry 1966, p. 429). The lectotype is Nat. Mus. Victoria No. P14238, figured by T. S. Hall (1899, pl. 17, fig. 7), from La2 near Lancefield, Victoria, Australia.

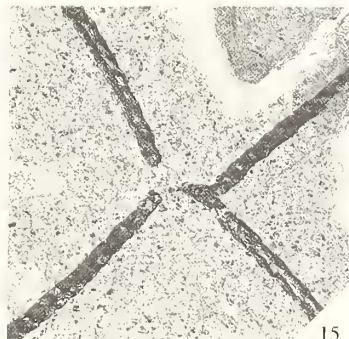
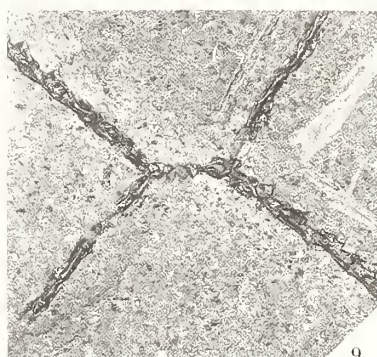
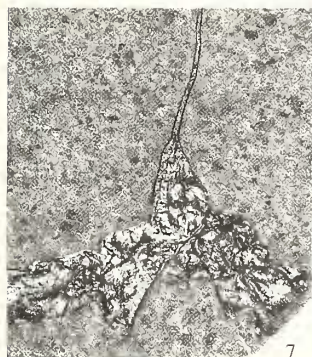
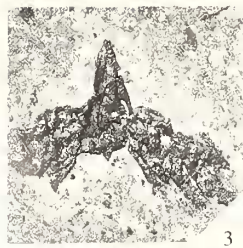
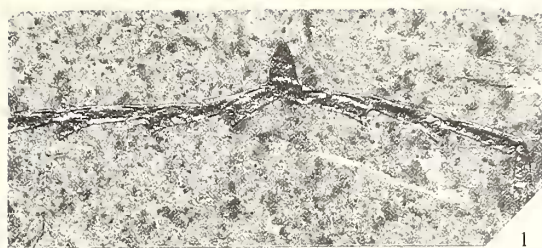
Diagnosis (revised, incorporating Berry's redescription of type material). Rhabdosome with two (or occasionally more) long, slender, gently declined stipes, straight or dorsally convex, widening rapidly from 0.4–0.6 mm proximally to a maximum of 0.5–0.9 mm. Sicular inclined, 1.0–1.5 mm long, 0.25–0.3 mm wide at aperture. Autothecae number 9–9.5 in 10 mm, overlapping two-fifths to one half of their total length, inclined at about 10° to dorsal margin. Bithecae apparently absent except for sicular bitheca.



TEXT-FIG. 6. *Kiaerograptus pritchardi* (T. S. Hall, 1899), GP38, all $\times 5$ except A ($= \times 10$). A and B, GSC 87381. C, GSC 87393. D, GSC 87390. E, GSC 87412. F, GSC 87383 (also figured Pl. 1, fig. 1). G, GSC 87368. H, GSC 87378. I, GSC 87411. J, GSC 87399. K, GSC 87406. L, GSC 87407.

EXPLANATION OF PLATE I

- Fig. 1. *Kiaerograptus pritchardi* (T. S. Hall, 1899). GSC 87383, GP38, $\times 10$ (also figured Text-fig. 6F).
 Figs 2–4. *Kiaerograptus undulatus* sp. nov. MPS42C, $\times 10$. 2, GSC 87286. 3, GSC 87330 (also figured Text-fig. 8o). 4, GSC 87327.
 Figs 5–7. *Kiaerograptus magnus* sp. nov. GP38, $\times 10$. 5, GSC 87388. 6, GSC 87331. 7, GSC 87361 (also figured Text-fig. 8N).
 Figs 8 and 9. *Kiaerograptus bulmani* (Thomas, 1963). MPS42C, $\times 5$. 8, GSC 87329. 9, GSC 87317.
 Figs 10–16. *Paratemnograptus isolatus* gen. et sp. nov. 10, GSC 87375, GP38, $\times 10$. 11, GSC 87315, MPS42C, $\times 10$. 12, GSC 87287, CHN8.30, $\times 5$. 13, GSC 87384b, detail of distal branching, GP38, $\times 5$. 14, GSC 87288, CHN8.30, $\times 2.5$. 15, GSC 87385, GP38, $\times 2.5$. 16, GSC 87289, CHN8.30, $\times 5$.



Material and localities. Many flattened, non-isolated specimens from GP38; others from MPN17A, 17B. One possible poor isolated specimen from MPS42C.

Description. The rhabdosome consists of two slender stipes occasionally reaching over 35 mm long; second order branching has not been observed in our material. The stipes are 0.3–0.5 mm (commonly 0.4 mm) wide at $th1^1$, increasing only slightly to a maximum 0.5 mm (cf. type material). Narrow widths are probably due to preservation in oblique orientation, the larger measurements probably being more representative of the true widths.

The sicula is 1.0–1.15 mm long (cf. 1.4 mm for type material), is usually inclined rather than perpendicular to the stipes, and has a gentle convex curvature with respect to the rutellar margin. The aperture shows a pronounced rutellum and is typically 0.25 mm wide. $Th1^1$ presumably buds from the prosicula, growing down along the rutellar margin for 0.75–0.85 mm before turning sharply out and growing slightly downwards for the remainder of its 0.6–0.8 mm length. The base of the rutellar margin of the sicula is left free for 0.15–0.4 mm (commonly 0.2 mm), whereas the ventral wall of $th1^1$ subtends an angle of 60–80° with the sicular axis. The sicular bitheca has not been observed unequivocally, but by comparison with other taxa is almost certainly present. One specimen appearing to show a sicular bitheca reveals it to extend only slightly beyond the point where the ventral wall of $th1^1$ diverges from the sicula, probably explaining its cryptic form.

$Th1^2$ buds from $th1^1$ high on the reverse side, growing initially across the sicula in an almost horizontal direction before turning down to run along the antirutellar margin. It remains in contact with this margin until the sicular aperture is reached, at which point $th1^2$ bends abruptly out, subtending an angle of 50–60° with the sicular axis. This angle is maintained for 0.6–0.9 mm until the aperture is reached.

Remaining autothecae are almost straight, inclined at 10–15° with the dorsal stipe margin, but with a slightly concave ventral wall and gently flared aperture in most specimens. Occasionally, however, the ventral wall is straight; it is possible that the flaring is a preservational artefact related to differential lateral spread on flattening. Apertures are simple but deep, occupying one half to two-thirds of total stipe width. Thecal overlap represents a little under one half total thecal length, while thecal density is an almost constant 8–10 in 10 mm throughout the rhabdosome. Autothecal length appears to be related to size of rhabdosome, but it is unclear whether thecal growth is continuous throughout astogeny as demonstrated for several Arenig dichograptids by Williams and Stevens (1988a). Bithecae have not been observed apart from that of the sicula, and it is unlikely that they existed.

Remarks. Erdtmann *et al.* (1987) referred *K. pritchardi* to their new genus *Paradelograptus*; this genus is, however, characterized by slender thecae similar to *Adelograptus* and *Kinnegraptus* and lacks a sicular bitheca.

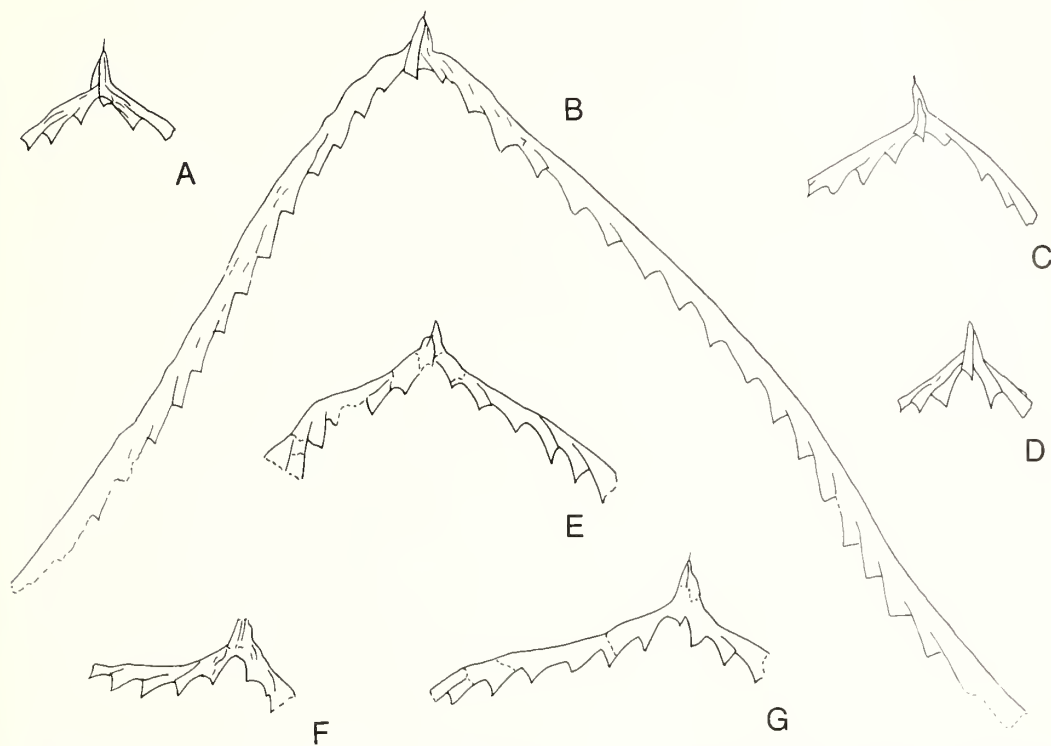
K. pritchardi appears to be a well-defined, consistent species with little variation in rhabdosome form and dimensions, in contrast to most other coeval taxa. It is easily separated from these by its distinctive proximal region. The Newfoundland representatives of *K. pritchardi* have rather smaller dimensions than those recorded by Berry (1966) for the type specimens. Berry recorded proximal widths of 0.7–0.8 mm widening to a maximum 0.8–0.9 mm in his text descriptions, but measurements from his illustrations and Cooper's (1979a, fig. 17k) figure of the lectotype demonstrate proximal widths of 0.6 mm. As noted above, thecal length (and consequently stipe width) appears to have increased during growth of the rhabdosome. As the type specimens have much longer stipes than our specimens, stipe widths between the two populations are considered to be compatible, while thecal densities are identical. The length of the sicula does, however, appear to be consistently longer in the type material (1.4 mm) than in the Newfoundland specimens (1.0–1.15 mm).

The single specimen of *Didymograptus tenuiramis* figured by Obut and Sobolevskaya (1962) is poorly preserved and seems to have suffered tectonic deformation. It does, however, appear very similar to *K. pritchardi* and is here tentatively referred to this species. Although Obut and Sobolevskaya (1962, fig. 4) refer the interval yielding *D. tenuiramis* to earliest Arenig, the associated assemblage could equally well be placed in the late Tremadoc as it contains '*Temnograptus*' species and predates the first occurrence of *T. approximatus*.

Specimens from the Yukon, northern Canada which Jackson (1974) referred to a new species *Didymograptus(?) stelki*, agree even more closely with the Australian types of *K. pritchardi* than those from Newfoundland, and we have no hesitation in assigning them to this species.

Most of our specimens of *K. pritchardi* originate from Green Point, where the late Tremadoc

interval is represented by a succession of fine-grained, fissile shales deposited in a rather deeper, more distal environment than elsewhere in the Cow Head Group. This distribution may be related to original environmental restraints, or may be due to poor preservation in rather coarser lithologies elsewhere. A similar problem exists for slender Arenig graptoloids in the Cow Head group, *Kinnegraptus* and *Adelograptus* being largely restricted to the more distal, fine-grained facies, deposited in deeper water.



TEXT-FIG. 7. *Kiaerograptus* cf. *K. taylori* (T. S. Hall, 1899), $\times 5$. A-D, GP38; A, GSC 87369; B, GSC 87386; C, GSC 87392; D, GSC 87410. E-G, MPS42C; E, GSC 87356; F, GSC 87357; G, GSC 87358.

Kiaerograptus cf. *K. taylori* (T. S. Hall, 1899)

Text-fig. 7A-G

cf. 1899 *Didymograptus taylori*, n. sp.; T. S. Hall, pp. 167-168, pl. 17, figs 11 and 12.

cf. 1960 *Didymograptus taylori* T. S. Hall; Thomas, pl. 1, fig. 15.

Material and localities. Seven flattened, non-isolated specimens from GP38 and MPS42C.

Description. The rhabdosome is composed of two stipes up to 25 mm long, with a deflexed or declined form and separated by an angle of $90-120^\circ$. They measure 0.6-0.8 mm wide at the first thecal aperture; the larger width is found in specimens with longer thecal lengths and higher inclinations to the dorsal stipe wall, but may be related to lateral spread in some instances. The stipes soon attain their maximum width of 1.0 mm, which is then maintained throughout the rhabdosome.

The sicula is a consistent 1.5-1.6 mm long, with an apertural width of 0.3-0.45 mm. It is initially straight, but has a convex curvature with respect to the rutellar margin over the distal 0.5 mm. A short nema is occasionally present; the sicular bitheca has not been seen, but is almost certainly present. Proximal

development has not been observed, but is probably similar to other late Tremadoc graptolites with a prosicular origin for th1¹. With the exception of the sicula, bithecae appear to be absent.

Autothecae have a low initial inclination of about 10° to the dorsal margin, but this increases throughout their length to reach a maximum of 30–40° near the aperture. Thecal length is somewhat variable; overlap is about one half of total length in early thecae, reducing to about one third distally. Free ventral thecal margins are markedly concave, particularly towards the apertures which occupy one third to one half of total stipe width, giving a markedly denticulate appearance to the ventral stipe margin. Thecal density is somewhat variable 8–10 in 10 mm proximally, but reduces to a constant 8 in 10 mm distally.

Remarks. Although the generic assessment of *K. taylori* has been discussed relatively recently (e.g. by Cooper and Stewart 1979, p. 790), no additional specimens appear to have been described since the original description by T. S. Hall in 1899. From his remarks (1899, p. 168) it seems that Hall possessed more than the one specimen illustrated; unfortunately there are several discrepancies between his written description, figure at natural size and the illustration recorded as $\times 3$ magnification. Thomas (1960, fig. 15) has since provided a rather clearer figure of the specimen at natural size.

Because of Hall's poor original description and lack of revisions using the type material, assignment of our Newfoundland specimens cannot be certain and we therefore refer them to *K. cf. taylori*. This species is unlike any other taxa from the late Tremadoc of the Cow Head Group, with the exception of *K. pritchardi*, from which it differs by its longer sicula, more robust form, steeply inclined stipes and narrower thecal apertures. Bulman (1950) compared his new species *Didymograptus primigenius* with *D. taylori*; the overall dimensions and rhabdosome form of this taxon from the middle Tremadoc of Quebec are, however, closer to those of *K. pritchardi*. It is distinguished from this species by its more steeply inclined thecae and higher thecal density of 11 in 10 mm.

Kiaerograptus undulatus sp. nov.

Plate 1, figs 2–4; Plate 3, figs 1 and 2; Text-fig. 8A–H

cf. 1937 *Didymograptus norvegicus*, n. sp.; Monsen, pp. 176–177, pl. 2, figs 7 and 8; pl. 4, figs 4 and 5; fig. 6.

1983 ?*Kiaerograptus* sp. cf. *K. quasimodo* Rushton; Henderson, p. 155, fig. 5g–j.

Derivation of name. From *undulatus* (Latin) meaning 'wavy', referring to the folded dorsal stipe margin.

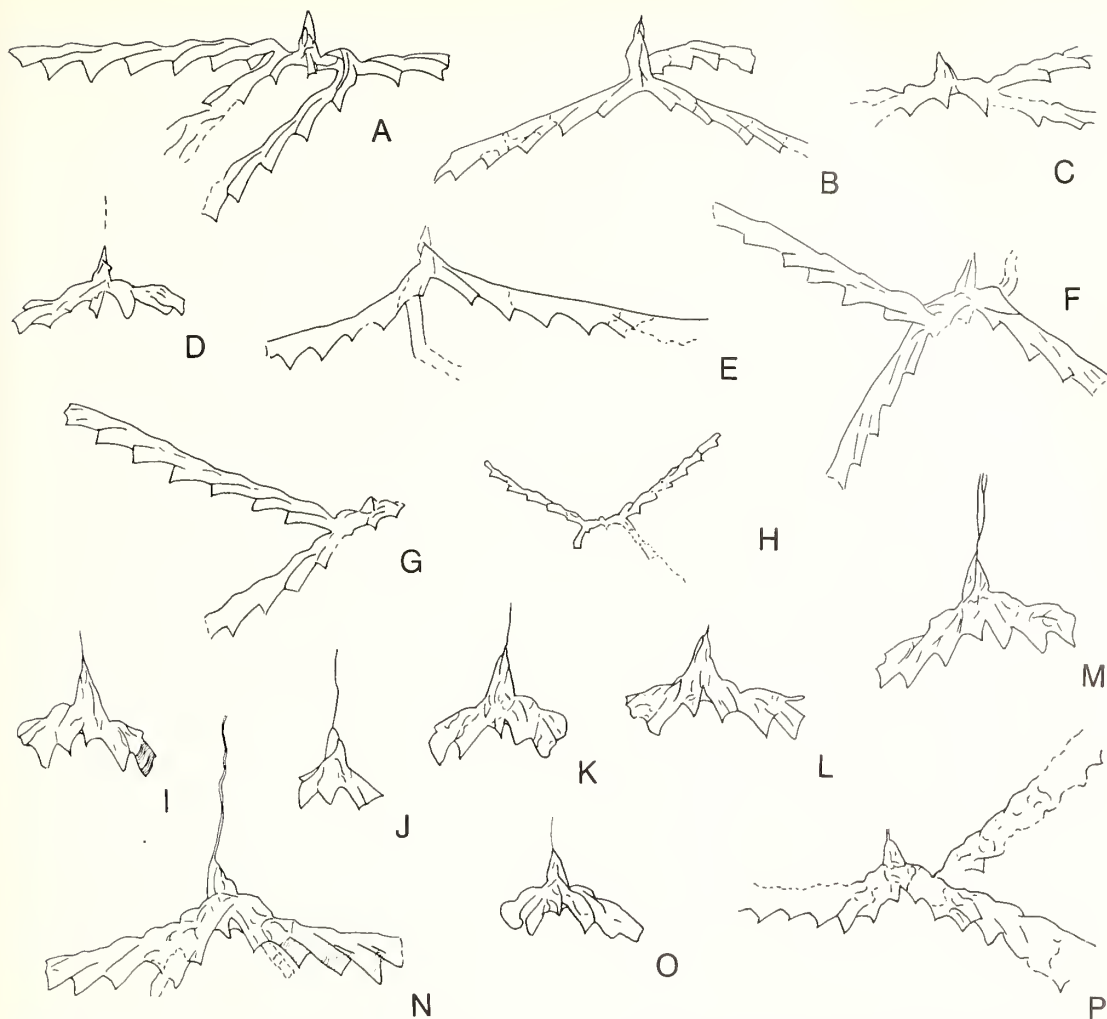
Type specimen. The holotype is GSC 87413, from Green Point (GP40). Figured Text-figure 8A.

Diagnosis. Small rhabdosome composed of four (occasionally two or three) slightly declined, radiating stipes, measuring 0.7–0.8 mm wide proximally with rapid increase to the maximum 1.0 mm. Sicula 1.5–1.8 mm long, almost straight, with apertural width of 0.25 mm. Prominent sicular bitheca filling much of 'notch' of basal rutellar margin. Autothecae strongly curved, with strong prothecal folds, wide apertures occupying one half of total stipe width and numbering 9–10 in 10 mm. Many or all autothecae with bithecae opening into large apertures.

Material and localities. Fifteen flattened, non-isolated specimens from GP38, 40; MPS42C; CH8-34. One isolated, three-dimensional specimen from MPS42C.

Description. The species is known only from small proximal fragments with stipes up to 8 mm long. The rhabdosome typically consists of four, gently declined, radiating stipes, formed by the dichotomous division of th2¹ and 2². Occasional specimens with two horizontal stipes considered to belong to this species have, however, been found. Stipes are generally 0.7–0.8 mm wide proximally, with rapid increase to 1.0 mm, although a few specimens are 1.0 mm wide proximally. The dorsal stipe margin is characterized by pronounced prothecal folds, although these are less conspicuous in more poorly preserved, flattened material.

The sicula is 1.5–1.8 mm long and almost straight throughout its entire length, with an apertural width of 0.25 mm. Proximal development has not been observed clearly, but evidently agrees with that of other late



TEXT-FIG. 8. A-H, *Kiaerograptus undulatus* sp. nov., A-G $\times 5$, H $\times 2.5$. A, GSC 87413, Holotype, GP40. B, GSC 87296, CHN8.34. C, GSC 87318, MPS42C. D, GSC 87328, MPS42C. E, GSC 87359, MPS42C. F, GSC 87371, GP38. G, GSC 87414, GP40. H, GSC 87322, MPS42C. I-P, *Kiaerograptus magnus* sp. nov. I-N GP38, $\times 5$; I, GSC 87365; J, GSC 87404; K, GSC 87363; L, GSC 87372; M, GSC 87408; N, GSC 87361, Holotype (also figured Pl. 1, fig. 7). O, GSC 87330, MPS42C (also figured Pl. 1, fig. 3). P, GSC 87325, MPS42C.

Tremadoc taxa. Th1¹ diverges from the sicula relatively high, leaving the basal rutellar margin free for 0.5–0.6 mm. Much of this ‘notch’ is, however, commonly filled by the sicular bitheca, giving a more robust and ‘filled-in’ appearance to the proximal region. Th1² also leaves the sicula above the level of the sicular aperture, leaving the antirutellar margin free for 0.1–0.2 mm.

The free ventral margins of th1¹ and 1² measure 1.0 mm and 0.8 mm respectively; both show pronounced downward curvature throughout their free portions and splay out towards the apertures, which are 0.35–0.4 mm in diameter (half total stipe width). Th2¹ and 2² are commonly dichotomous, giving rise to the typically ‘tetragraptid’ form; in these specimens th1¹ and 1² possess bithecae which open into large apertures alongside those of the autothecae and directly below the point of branching. It is unclear whether these bithecae are present in the two-stiped forms, or whether they occur throughout the rhabdosome. End-on views of the single isolated specimen suggest that they are indeed present in at least the succeeding few thecae, unless this specimen

is showing a third-order dichotomy. All autothecae throughout the rhabdosome show the same characteristic strong curvature, prothecal folds and wide apertures occupying one half of total stipe width. Thecal overlap is greater than one half, while thecal density is a constant 9–10 in 10 mm.

Remarks. *K. undulatus* is a very distinctive form when well preserved owing to the sinuous nature of the thecae, which gives an appearance reminiscent of the Arenig sinograptids. The outline of the dorsal wall is somewhat variable, from specimens with strong prothecal folds to others with an almost straight dorsal margin. Although this may be partly an original morphological feature, the folds may well have been reduced by differential lateral spread on compaction, as described for the Upper Ordovician *Dicellograptus complanatus* Lapworth by Briggs and Williams (1981) and Williams *et al.* (1982).

Henderson's (1983) specimens of *K.?* cf. *quasimodo* agree well with *K. undulatus*, although they are all two-stiped forms. The types of *K.?* *quasimodo* described by Rushton (1981) from the middle or upper Tremadoc subsurface of central England differ, however, by their longer sicula and more steeply inclined thecae, resulting in a slightly higher thecal count. Most specimens of *K.?* *quasimodo* were two-stiped forms, although one possible three-stiped specimen with a higher thecal density was recorded by Rushton (1981, fig. 3c). *K.?* *quasimodo* is clearly similar to *K. undulatus* and may well represent an ancestral taxon. *K. undulatus* is also comparable with *Didymograptus norvegicus* Monsen: this has a folded dorsal margin and equivalent thecal densities, but a rather smaller, inclined sicula 1.4 mm long and two reclined stipes.

The only other associated species with which *K. undulatus* may be confused is *K. buluauai* sp. nov. The latter species has a much more slender and open rhabdosome, rather more gently inclined thecae with a marginally lower thecal density of 8–9 in 10 mm, and seems to lack the prominent folded dorsal margin (although one two-stiped specimen possibly referable to this species does have prothecal folds).

Kiaerograptus magnus sp. nov.

Plate 1, figs 5–7; Plate 3, figs 4 and 7; Text-fig. 7I–P

Derivation of name. From *magnus* (Latin) meaning 'large', in reference to the large and robust sicula and proximal region.

Type specimen. The holotype is GSC 87361, from Green Point (GP38). Figured Plate 1, fig. 7 and Text-figure 8N.

Diagnosis. Robust rhabdosome with four, three or two stipes 1.2 mm wide proximally. Sicula up to 2.3 mm long, almost straight, with pronounced rutellum and aperture 0.5 mm diameter. Autothecae simple, inclined at 30–40° to dorsal margin, numbering 9–10 in 10 mm. Bithecae apparently lacking with exception of large sicular bitheca.

Materials and localities. Ten flattened specimens from MPS42C and GP38. Four isolated, three-dimensional specimens from SPI43 and MPS42C.

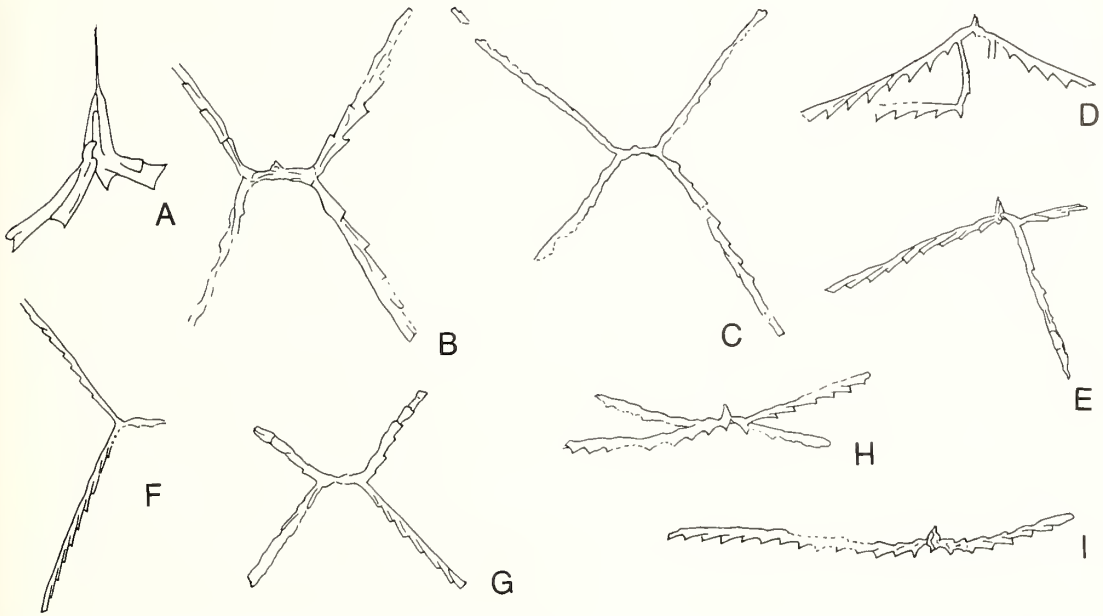
Description. The rhabdosome is robust with two, three or four stipes, 1.2 mm wide proximally and increasing rapidly to over 1.5 mm within 5 mm. Only proximal fragments have been positively identified, with stipes up to 6 mm long.

The sicula is long and wide, reaching up to 2.3 mm long measured along the gently convex rutellar margin, with a conspicuous rutellum projecting 0.2 mm and long nema which is occasionally thickened or forked (Text-fig. 8M, N). The sicula is 0.5 mm diameter at its aperture. $th1^1$ buds from the prosicula, growing down in contact with the metasicula for about 1 mm before diverging gently out at 20–30°. A large sicular bitheca fills most of the notch left between the rutellar margin of the sicula and ventral wall of $th1^1$. The arrangement of the sicula and first theca is highly symmetrical in young growth stages, giving an appearance approaching that found in the Arenig genus *Isograptus*. This symmetry is, however, lost during astogeny, as $th1^1$ continues to grow with a free ventral wall up to 1.1 mm long.

Th1² buds from high up th1¹, as does Th2¹. It grows down and across the sicula, its ventral wall intersecting the antirutellar apertural margin of the sicula. Its original angle of 30° subtended with the sicular axis decreases slightly throughout its distal portion, resulting in a concave free ventral margin up to 1.0 mm long.

Remaining development is similar to other *Kiaerograptus* taxa, th2¹ and 2² normally being dichotomous, although one or both dichotomies may be suppressed. Remaining autothecae are straight and inclined at 30–40° to the dorsal margin. They overlap about one half their length, have simple apertures occupying about one half of total stipe width, and number 9–10 in 10 mm. No bithecae have been observed apart from that of the sicula.

Remarks. The robust proximal region and large sicula separate *K. magnus* from all other coeval *Kiaerograptus* species and give an appearance reminiscent of *Clonograptus*. However, *K. magnus* lacks the common bithecae characteristic of this genus during the late Tremadoc, and appears to only have a maximum of four stipes, although more complete specimens might potentially possess further delayed, dichotomous branching. The forked and thickened nemata present on some specimens are unusual for graptolites from this stratigraphical interval and may have some taxonomic significance.



TEXT-FIG. 9. A–H, *Kiaerograptus bulmani* (Thomas, 1973). A, GSC 87400, GP38, $\times 10$; B, GSC 87420, GP40, $\times 5$; C–H, $\times 2.5$; C, GSC 87324, MPS42C; D, GSC 87339, MPS42C; E, GSC 87295, CHN8.34; F, GSC 87364, GP38; G, GSC 87366, GP38; H, GSC 87319, MPS42C. I, *K. bulmani* (Thomas, 1973)?, GSC 87323, MPS42C, $\times 2.5$.

Kiaerograptus bulmani (Thomas, 1973)

Plate 1, figs 8 and 9; Plate, 3 figs 5, 6, 8–14; Text-fig. 9A–I

- 1971 *Tetragraptus otagoensis* (Benson and Keble); Erdtmann, pp. 259–260, pl. 33, figs 1–3.
- 1973 *Tetragraptus bulmani* sp. nov.; Thomas, pp. 530–531, pl. 2, figs *b* and *c*.
- 1979 *Tetragraptus bulmani* Thomas; Cooper and Stewart, p. 795, text-fig. 8*h, k*.

Type specimen. The holotype is specimen No. 64419 in the Mines Department Museum, Melbourne. From the middle Lancefieldian (La2), loc. 68, Staurograptus Gully, Parish of Springfield, Victoria.

Diagnosis (revised, incorporating descriptions by Thomas (1973) and Cooper and Stewart (1979)). Small, slender rhabdosome with four or three, radiating, gently declined stipes increasing from 0.4–0.5 mm wide proximally to a maximum 0.8 mm (0.5–0.6 mm in scalariform or oblique preservation). Thecae simple, straight, gently inclined at about 20° and numbering a constant 8–10 in 10 mm. Sicula with bitheca, other bithecae apparently lacking except at dichotomies.

Material and localities. Twenty flattened specimens from CH8/34; MPS42C; GP38, 40. Fifteen isolated, three-dimensional specimens from SPI43, MPS42C and GP38.

Description. The rhabdosome is composed of four radiating, slender stipes up to 20 mm long. Proximally they have a dorso-ventral width of 0.4–0.5 mm, increasing to 0.5–0.7 mm in 5 mm and reaching a maximum of 0.8 mm. Stipes are commonly preserved in oblique or scalariform view, resulting in rather narrower widths of 0.5–0.6 mm. Rare preservation of the rhabdosome in lateral view reveals the stipes to be gently declined. Occasionally one dichotomy is suppressed, resulting in a three-stiped rhabdosome, although the majority of specimens from the Cow Head Group possess four stipes. One specimen possibly referable to *K. bulmani* (Text-fig. 9i) has only two, horizontal stipes, suggesting suppression of both dichotomies; this example however has a strongly folded dorsal margin and may not belong to this species.

The sicula is 1.4 mm long (but apparently only 1.2 mm in non-isolated specimens), measured along the rutellar margin, with an apertural diameter of 0.2–0.25 mm. It is straight or almost straight throughout its length, with a small but conspicuous rutellum projecting 0.08 mm beyond the antirutellar, apertural margin. Th1¹ buds from the prosicula on the rutellar side and grows down in contact with the sicula for 0.8–0.85 mm before turning out, after which it subtends an angle of 40° with the sicular axis for the remaining 0.7–0.9 mm of its length. Th1¹ has an almost constant diameter of 0.2–0.23 mm during the second portion of its development and opens into a simple aperture.

A sicular bitheca is invariably present, opening at a level varying from 0.15 mm above the point of divergence of th1¹ to just below the level of divergence. Development may be sinistral or dextral. Th1² buds from th1¹ about 0.5 mm below the apex of the sicula; it grows down and across at 30° to the sicular axis, maintaining this direction of growth throughout its length. Subsequent development and branching patterns appear to be typically 'dichtograptid', with th1², th2¹ and th2² dichotomous (one or both branchings may be suppressed). Bithecae appear to be absent apart from that of the sicula, and possibly at dichotomies (Plate 3, fig. 13).

Remaining thecae are simple, straight, gently inclined at about 20° to the dorsal margin and have apertures occupying one third to one half of total stipe width. Thecal overlap is about one-third, while thecal density is a uniform 8–10 in 10 mm throughout the rhabdosome. Rare flattened specimens appear to exhibit prothecal folds, but these are not present in isolated material. Critical observation suggests that they may be due to lateral spread of the apertural regions during flattening in oblique or scalariform orientation, apertural walls becoming visible on both sides of the stipe margin (e.g. Text-fig. 9B, G).

Remarks. *K. bulmani* is distinct from other taxa at this stratigraphical level due to its narrow stipes and widely spaced thecae. Our specimens appear to agree with the Australian types in all respects, except in lacking flared thecal apertures. Such flaring is, however, common in many graptolites with straight, simple thecae, due to post-mortem, differential lateral spread during flattening of the rhabdosome and is, therefore, of no taxonomic importance. *K. bulmani* differs from *Kiaerograptus otagoensis* (Benson and Keble, 1936) by its rather narrower stipes and lower thecal densities; Erdtmann's (1971) specimens referred to *K. otagoensis* are from Martin Point and clearly belong to *K. bulmani*. *K. bulmani* may be distinguished from *K. undulatus* sp. nov. by that species' rather different proximal development, wider stipes and prominent prothecal folds. Occasionally, however, specimens are found preserved in oblique or scalariform orientation which could be assigned to either one of the species.

The similarity in thecal style between *K. bulmani* and *Kiaerograptus pritchardi* (T. S. Hall) was noted both by Thomas (1973) and by Cooper and Stewart (1979). Our isolated and flattened material reveals that *K. bulmani* has a similar proximal development to that shown by both *K. pritchardi* and *K. taylori*, which is why we refer that species to *Kiaerograptus* rather than retaining within the dichograptid genus *Tetragraptus*. *K. otagoensis* is also similar and should be referred to this genus. Cooper and Stewart (1979) remarked that *K. bulmani* was rather similar to the

Bendigonian (lower Arenig) species *Tetragraptus harti* T. S. Hall. Williams and Stevens (1988a) recently redescribed this taxon from the *D. bifidus* Zone of the Cow Head Group and transferred it to the genus *Etagraptus*. Although similar in overall rhabdosome form, *E. harti* is a true dichograptid without a sicular bitheca, and any similarity to *K. otagoensis* is entirely homoeomorphic.

Genus PARATEMNOGRAPTUS nov.

Type species. Paratemnograptus isolatus sp. nov. By monotypy.

Diagnosis. Pauciramous, radiate rhabdosome with up to sixteen stipes arising from two primary stipes by three orders of widely spaced, delayed, irregular, dichotomous branching. Sicula with bitheca. Autothecae gently curved with moderate inclination, simple apertures and apparently lacking bithecae.

Remarks. Proximal branching conforms to a standard tetragraptid plan, with two primary stipes and th²₁ and th²₂ dichotomous. Subsequent dichotomies are delayed and irregular, many large rhabdosomes possessing only four stipes. Overall form may, therefore, be similar to either *Tetragraptus* or *Temnograptus*, although both these genera are Arenig in age and lack bithecae. *Paratemnograptus* further differs from the diagnosis of *Temnograptus* given by Bulman (1970, p. V113) in having irregular dichotomous stipe division and non-denticulate thecae. The type species of *Temnograptus*, namely *T. multiplex* (Nicholson, 1868), is poorly known and based on inadequate, flattened and deformed material from an uncertain stratigraphic level. Further work may ultimately prove *Paratemnograptus* to be synonymous with Nicholson's genus.

Paratemnograptus isolatus sp. nov.

Plate 1, figs 10–16; Plate 2, fig. 4; Plate 4, figs 1–8; Text-fig. 10A–O

- ?1899 *Tetragraptus decipiens*, n. sp.; T. S. Hall, pp. 168–169, pl. 17, figs 13–15; pl. 18, figs 16–19.
- ?1904 *Temnograptus noveboracensis* sp. nov.; Ruedemann, pp. 619–620, pl. 5, figs 15–20, 35, 36.
- ?1920 *Tetragraptus decipiens*, T. S. Hall; Keble, pp. 199–200, pl. 34, fig. 1a–e.
- ?1947 *Temnograptus noveboracensis* Ruedemann; Ruedemann, p. 284, pl. 44, figs 14–16; pl. 45, figs 1–4.
- ?1962 *Temnograptus* aff. *noveboracensis* Ruedemann; Obut and Sobolevskaya, p. 79, pl. 3, fig. 3.
- ?1966 *Tetragraptus decipiens* T. S. Hall; Berry, pp. 423–424, pl. 44, figs 5, 10, 11.
- ?1969 *Tetragraptus decipiens* T. S. Hall; Bulman and Cooper, pp. 215–216, pl. 1, figs 1–4; fig. 3a–c.
- ?1974 *Clonograptus* sp. A; Jackson, pp. 46–47, text-fig. 4.
- 1974 *Clonograptus* sp. B; Jackson, p. 47, text-fig. 1m, n.
- ?1974 *Tetragraptus decipiens* T. S. Hall; Jackson, pp. 53–54, pl. 5, fig. 4.
- 1979a *Temnograptus* aff. *regularis* (Törnquist, 1904); Cooper, p. 58, pl. 1f; fig. 24.
- ?1979b *Tetragraptus decipiens* T. S. Hall; Cooper, fig. 5f.
- 1979 *Temnograptus* sp.; Cooper and Stewart, pp. 793–795, text-fig. 8c.
- ?1979 *Tetragraptus decipiens* T. S. Hall; Cooper and Stewart, pp. 795–796, text-fig. 8a, b.
- ?1982 *Temnograptus* sp.; Gutierrez-Marco, fig. 2k.

Derivation of name. From *isolatus* (Latin) meaning detached or separate, in reference to the widely spaced, irregular dichotomous branching.

Type specimen. The holotype is GSC 87284, from the Ledge, Cow Head Peninsula (CHN8.30). Figured Text-fig. 10L.

Diagnosis. Large rhabdosome with four to sixteen slightly flexuous, radiating stipes increasing rapidly from 0.8–1.2 mm wide proximally to 1.4 mm maximum. Slender sicula with sicular bitheca,

funicle composed of $th1^1$ and $th1^2$ 2.5–3.0 mm wide. Thecae simple, overlap one half, thecal density 9–10 in 10 mm.

Material and localities. Numerous flattened specimens from CHN8.30; MPN17B; MPS42C; GP38, 40. Over twenty isolated, three-dimensional specimens from SPI43, MPS42C.

Description. The rhabdosome consists of four to sixteen long, slightly flexuous, radiating stipes reaching over 70 mm long and widening rapidly from 0.8–1.2 mm proximally to a maximum 1.4 mm which is then maintained.

The sicula is 1.6–1.8 mm long; it is straight throughout its length and relatively slender, reaching 0.2 mm diameter at the aperture. It has a small but conspicuous rutellum extending 0.1–0.15 mm beyond the antirutellar margin. $Th1^1$ generally buds from the prosicula on the rutellar margin, although in one well-preserved specimen it buds from the antirutellar side, then swings immediately across to the rutellar margin. $Th1^1$ grows down along the rutellar margin for 0.75 mm before turning outwards, subtending an angle of 40° with the sicular axis which is maintained throughout the remainder of its length. The distal rutellar margin of the sicula is left free for 0.25–0.3 mm. A sicular bitheca buds from the sicula below the point of origin of $th1^1$, opening into an aperture a little above the point of divergence of the ventral wall of $th1^1$ from the sicula. Development may be either right- or left-handed; $th1^2$ buds from $th1^1$ above its point of deflection, growing down and across the sicula and the ventral wall of $th1^2$ intersects the base of the antirutellar sicula margin. $Th1^2$ is dichotomous, giving rise to $th2^1$ and $th2^2$, as are each of these subsequent thecae to give the typical 'tetragraptid' proximal plan. The funicle, consisting of the first two thecae, is 2.5–3.0 mm wide.

Subsequent autothecae have a typically dictyograptid appearance; their angle of inclination with the dorsal margin increases from 30° initially to 50° towards the aperture, which is simple. Thecal overlap is one half of total length, while apertures occupy one half to two-thirds of total stipe width. Bitheca appear to be lacking with the exception of the sicular bitheca. Thecal density is a uniform 9–10 in 10 mm throughout the rhabdosome.

Remarks. Although the overall form is distinctive, details of thecal morphology or proximal development are rarely seen in flattened specimens owing to common preservation in scalariform orientation. Most rhabdosomes have only four stipes, but sufficient specimens have been found with additional distal dichotomies to determine the variability of this morphological feature. There are no other associated species which might be confused with *P. isolatus*; as can be seen from the list of synonymies, both the generic and specific identity of this taxon have, however, been problematic.

Temnograptus regularis (Törnquist) as described by Törnquist (1904) and Monsen (1937) certainly appears similar, but both our material and that described by Cooper (1979a) has more widely spaced dichotomies, more slender stipes and is much earlier (late Tremadoc as opposed to middle Arenig).

Temnograptus noveboracensis Ruedemann was based entirely on distal stipe fragments and is, therefore, not a strictly valid taxon. Ruedemann (1947, pl. 44, figs 14–16) did, however, figure three fragments from the Cow Head Group and these are likely to belong to *P. isolatus*.

Tetragraptus decipiens T. S. Hall has been recorded previously from the late Tremadoc and early

EXPLANATION OF PLATE 2

- Fig. 1. *Aorograptus victoriae* (T. S. Hall, 1899). GSC 87309, MPS42C, $\times 2.5$ (also figured Text-fig. 11L).
 Figs 2 and 3. *Adelograptus* cf. *A. tenellus* (Linnarsson, 1871). 2, GSC 87376, GP38, $\times 5$. 3, GSC 87307, MPN17B, $\times 10$.
 Fig. 4. *Paratemnograptus isolatus* gen. et sp. nov. GSC 87362, GP38, $\times 10$ (also figured Text-fig. 10B).
 Fig. 5. *Clonograptus* sp. B. GSC 87314, MPS42C, $\times 2.5$ (also figured Text-fig. 15f).
 Fig. 6. *Clonograptus* sp. A. GSC 87354, MPS42C, $\times 2.5$.
 Figs 7–11. *Rhabdinopora* sp. 7, GSC 87308, MPN17B, $\times 10$. 8, GSC 87290, CHN8.30, $\times 5$. 9, GSC 87291, CHN8.30, $\times 2.5$. 10, GSC 87396, GP38, $\times 5$. 11, GSC 87292, CHN8.30, $\times 2.5$. 13, GSC 87293, CHN8.30, $\times 2.5$.
 Fig. 12. Dendroid indet., distal fragment. GSC 87316, MPS42C, $\times 5$.



1



2



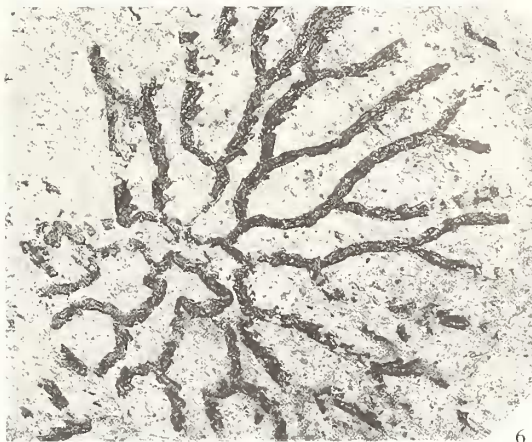
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4



5



6



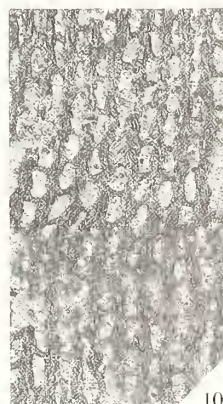
7



8



9



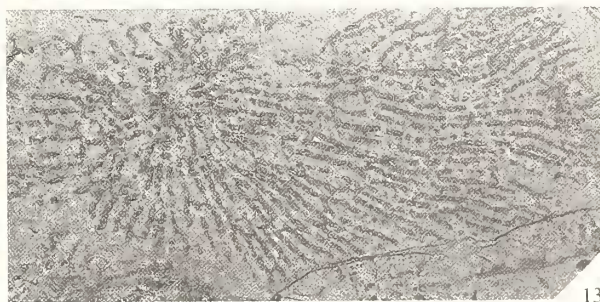
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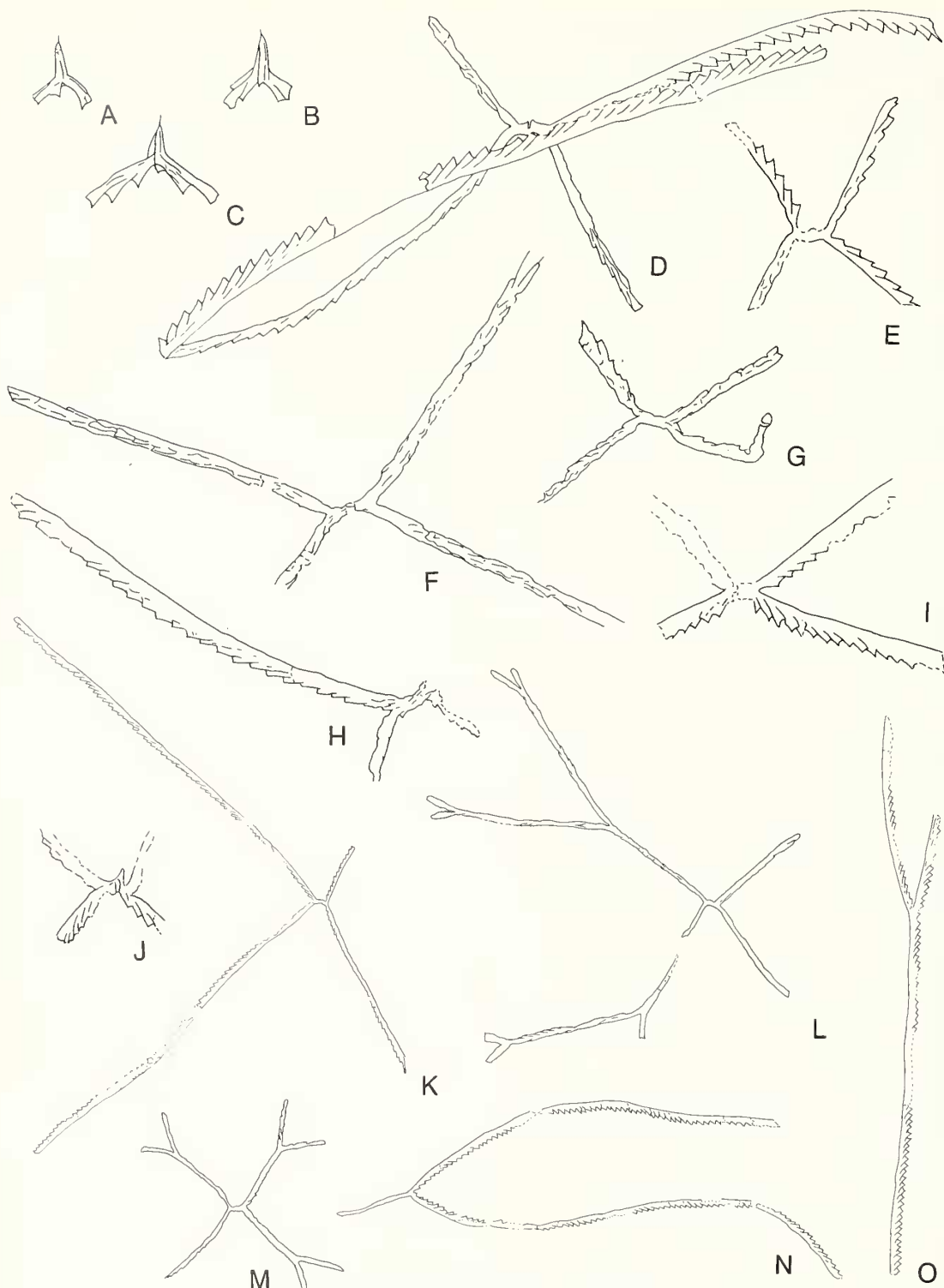
11



12



13



TEXT-FIG. 10. For legend see opposite.

Arenig of Australasia and North America; the type specimens are, however, poor and are only juveniles (see Berry 1966). The only description of *T. decipiens* including anything more than juveniles was by Keble (1920). The taxonomic affinities of *T. decipiens* were discussed by Williams and Stevens (1988a), who concluded that many lower Arenig specimens were probably juvenile representatives of *T. approximatus approximatus* Nicholson. We furthermore believe that the Tremadoc examples of *T. decipiens* are probably juvenile representatives of our new species *P. isolatus*, in which case *T. decipiens* would be a senior synonym. The dimensions of the sicula given by Berry (1966) for the types of *T. decipiens* are, however, greater than those for *P. isolatus*; he recorded that the sicula was 1.9–2.4 mm long and 0.4–0.5 mm wide at the aperture (cf. 1.6–1.8 mm long and 0.2 mm wide for *P. isolatus*).

Until a better population of *T. decipiens* is collected from the type locality, including large, mature rhabdosomes and specimens in which the presence or absence of a sicular bitheca can be determined, the synonymy with *P. isolatus* must remain questionable.

Genus AOROGRAPTUS nov.

Derivation of name. From *aoros* (Greek), meaning pendulous, hanging or waving, in reference to the pendent nature of the rhabdosome.

Type species. *Bryograptus victoriae* T. S. Hall, 1899, p. 165, pl. 17, figs 1 and 2.

Diagnosis. Pendent or declined rhabdosome with regular, commonly delayed, dichotomous branching from two primary stipes. Sicula and most autothecae with bithecae; autothecae composed of simple, dichgraptid-like tubes, commonly curved with fairly high distal inclinations, stipes relatively robust.

Remarks. Until more extensive taxonomic revision of Middle and Upper Tremadoc graptolites is accomplished, this genus is essentially monotypic. *A. victoriae*, the type species, has been previously assigned to both *Bryograptus* and *Adelograptus*. It differs from the former genus by having two, rather than three, primary stipes, and from the latter in having a relatively robust, large rhabdosome with regular branching. When preserved in radiate, rather than pendent, orientation, the rhabdosome gives an appearance which would normally have been referred to *Clonograptus*. As discussed elsewhere, we consider this genus to be a typically dichograptid, Arenig genus, lacking bithecae or any other 'dendroid' features (in the traditional sense). It is therefore likely that many specimens referred previously to *Clonograptus* are actually representatives of our new genus *Aorograptus* preserved in radiate (horizontal) orientation.

Several previous authors have referred to the possibility that *Bryograptus* evolved to give the lower Arenig dichograptid genus *Pendeograptus* and/or the pendent didymograptids (see Fortey and Cooper 1986 for discussion). In our opinion, it is likely that *Aorograptus* evolved from *Bryograptus* in the late Tremadoc through loss of one primary stipe and the stolon system, then subsequently gave rise to *Pendeograptus* through loss of bithecae and further stipe reduction. It is not, however, the ancestor of *Didymograptus* (*Didymograptellus*) Cooper and Fortey, 1982, which almost certainly evolved from the *Didymograptus* (*Expansograptus*) *nitidus* group of extensiform didymograptids (see Williams and Stevens 1988a).

TEXT-FIG. 10. *Paratennograptus isolatus* gen. et sp. nov., A–C $\times 5$, D–J $\times 2.5$, K–O $\times 1$. A, GSC 87301, MPN17B. B, GSC 87362, GP38 (also figured Pl. 2, fig. 4). C, GSC 87370, GP38. D, GSC 87333, MPS42C. E, GSC 87402, GP38. F, GSC 87280, CHN8.30. G, GSC 87281, CHN8.30. H, GSC 87382, GP38. I, GSC 87282, CHN8.30. J, GSC 87283, CHN8.30. K, GSC 87355, MPS42C. L, GSC 87284, Holotype, CHN8.30. M, GSC 87334, MPS42C. N, GSC 87415, GP40. O, GSC 87311, MPS42C.

Aorograptus victoriae (T. S. Hall, 1899)

Plate 2, fig. 1; Plate 3, fig. 15?; Plate 4, figs 9–14; Plate 5, figs 1–8; Text-fig. 11A–Q

- 1899a *Bryograptus victoriae*, n. sp.; T. S. Hall, p. 165, pl. 17, figs 1 and 2.
 1899a *Bryograptus clarki*, n. sp.; T. S. Hall, pp. 165–166, pl. 17, figs 3 and 4.
 1899b *Bryograptus victoriae*; T. S. Hall, p. 450, pl. 22, figs 11 and 12.
 1914 *Bryograptus* sp.; T. S. Hall, pl. 8, figs 5 and 6.
 1932 *Bryograptus victoriae* T. S. Hall; Harris and Keble, pl. 4, fig. 2.
 1933 *Bryograptus pauxillus* sp. nov.; Benson, p. 403 (*nom. nud.*).
 1936 *Bryograptus lunnebergensis* Moberg; Benson and Keble (*pars*), pp. 269–270, pl. 30, figs 1–11 (non pl. 30, figs 14 and 15 = *A. cf. tenellus* (Linnarsson)?).
 ?1936 *Bryograptus simplex* Törnquist; Benson and Keble, p. 270, pl. 30, figs 12 and 13.
 1938b *Bryograptus victoriae* T. S. Hall; Harris and Thomas, pl. 1, fig. 7.
 1938 *Bryograptus clarki* T. S. Hall; Harris and Thomas, pl. 1, fig. 8.
 1941 *Adelograptus victoriae* (T. S. Hall); Bulman, p. 115 (no description or figures, but refers to *Adelograptus* and synonymises *A. clarki*).
 1955 *Adelograptus asiaticus*; Mu, p. 30, pl. 10, figs 4–7.
 ?1955 *Adelograptus sinicus*; Mu, p. 30, pl. 10, fig. 8.
 1960 *Bryograptus victoriae* T. S. Hall; Thomas, pl. 1, fig. 6.
 1960 *Bryograptus clarki* T. S. Hall; Thomas, pl. 1, fig. 7.
 ?1960 *Adelograptus victoriae* (T. S. Hall); Berry, pp. 46–47 (remarks only, no descriptions or figures).
 1966 *Adelograptus clarki* (T. S. Hall); Berry, pp. 419–421, pl. 44, figs 2 and 4.
 1966 *Adelograptus victoriae* (T. S. Hall); Berry, pp. 421–422, pl. 44, fig. 1.
 1968 *Adelograptus kazakhstanensis* Tzaj, n. sp.; Tzaj, pp. 493–494, pl. 5, fig. 2.
 1968 *Bryograptus ulutanensis* Tzaj, n. sp.; Tzaj, p. 495, pl. 5, fig. 3.
 1969 *Bryograptus*? sp. of T. S. Hall; Bulman and Cooper, fig. 4a, b.
 1974 *Adelograptus victoriae* (T. S. Hall); Jackson, p. 45, pl. 5, fig. 2; text-fig. 2a.
 1974 *Adelograptus kazakhstanensis* Tzaj; Tzaj, pl. 37, pl. 1, figs 6 and 7.
 1974 *Bryograptus ulutanensis* Tzaj; Tzaj, pp. 38–39, pl. 2, figs 1–3; fig. 4.
 1974 *Bryograptus* sp.; Tzaj, p. 39, pl. 2, fig. 4.
 1979a *Adelograptus clarki* (T. S. Hall); Cooper, pp. 54–55, pl. 2a, b; fig. 19a–c.
 1979b *Adelograptus victoriae* (T. S. Hall); Cooper, fig. 5g.
 1979 *Adelograptus victoriae* (T. S. Hall); Cooper and Stewart, pp. 784–785, text-fig. 8g, j, l.
 1979 *Adelograptus asiaticus* Mu; Wang *et al.*, pp. 499–500, pl. 1, figs 6 and 7; fig. 8a–e.
 1979 *Adelograptus simplex* (Törnquist); Wang *et al.*, p. 501, fig. 9a.
 1979 *Adelograptus victoriae* (T. S. Hall); Wang *et al.*, p. 501, fig. 9b.

Type specimen. Nat. Mus. Victoria No. P14240 (figured by Hall 1899, pl. 44, fig. 1) was designated lectotype by Berry (1966, p. 421). From the middle Lancefieldian (La2) near Lancefield, Victoria, Australia.

Diagnosis. Pendent or declined rhabdosome with many stipes increasing from 0.6–0.8 mm wide proximally to a maximum 1.2 mm. Autothecae with concave ventral margin, flared aperture and with bithecae, thecal density increasing from 8 in 10 mm proximally to 10 in 10 mm distally.

EXPLANATION OF PLATE 3

- Figs 1 and 2. *Kiaerograptus undulatus* sp. nov. GSC 87436, MPS42C. 1, $\times 20$, 2, $\times 40$.
 Figs 3, 4, 7. *Kiaerograptus magnus* sp. nov. 3, GSC 87433, SPI43. 4, GSC 87474, MPS42C. 7, GSC 87473, MPS42C. All $\times 40$.
 Figs 5, 6, 8–14. *Kiaerograptus bulmani* (Thomas, 1963). 5, GSC 87462, GP38. 6, GSC 87434, SPI43. 8 and 9, GSC 87459, GP38. 10, GSC 87442, SPI43. 11, GSC 87443, SPI43. 12, GSC 87446, SPI43 (also figured Text-fig. 5A, B). 13, GSC 87488, MPS42C. 14, GSC 87444, SPI43. All $\times 40$.
 Fig. 15. *Aorograptus victoriae* (T. S. Hall, 1899)?, GSC 87465, MPS42C, $\times 40$.
 Scanning electron micrographs of isolated specimens.



WILLIAMS and STEVENS, *Kiaerograptus*, *Aorograptus*

Material and localities. Many isolated, three-dimensional and flattened, non-isolated specimens from all localities in the late Tremadoc of the Cow Head Group described in this paper.

Description. The rhabdosome has a pendent form with up to sixteen branches formed by four delayed dichotomies and sometimes exceeds 60 mm in diameter. Occasionally specimens are preserved flattened in horizontal orientation; in this instance the rhabdosome has a radiate, 'clonograptid' appearance. Stipe widths vary depending on astogeny, but are commonly 0.6–0.8 mm proximally, increasing distally to a maximum 1.2 mm.

The sicula is large, measuring 1.4–2.0 mm long; although such variation is not found in most other associated taxa, detailed observation has revealed continuous variation between the extremes and taxonomic division based solely on this criterion is therefore not warranted. The sicula is more or less straight, increasing gradually in diameter to 0.25–0.3 mm at the aperture. The nema is commonly preserved, reaching up to 4 mm long, and the rutellum is pronounced, extending 0.15 mm beyond the antirutellar margin.

Th¹ buds from the prosicula, growing down in contact with the rutellar margin for 0.75 mm before bending out at an angle of 70° to the sicular axis. It subsequently curves down throughout its length, ending subparallel to the sicular axis after 0.8–1.2 mm. The aperture has a short selvage and is 0.3–0.4 mm wide (one half to two-thirds total stipe width). A sicular bitheca buds from the sicula 0.5 mm below the point of origin of th¹. It varies tremendously in length, from little more than a concealed foramen to a theca with an aperture just above the point of divergence of the ventral wall of th¹. The distal notch between the rutellar margin of the sicula and th¹ is also rather variable in size, from 0.4–0.6 mm long.

Th² buds from th¹ not far below its point of origin, growing down and across the sicula at an angle of 20–30°. Development may be either dextral or sinistral. The ventral wall of th² intersects the antirutellar margin of the sicular aperture, after which the theca arches gently down towards the thecal aperture, the free portion of ventral wall measuring 0.8–1.0 mm. Th² is dicalycal, giving rise to both th²¹ and th²².

Th²¹ and th²² are also normally dicalycal, although one dichotomy is occasionally suppressed to give an asymmetrical branching pattern. Delayed but fairly regular dichotomous branching occurs throughout the rhabdosome, resulting in third or fourth order stipes in mature specimens. Each autotheca possesses a bitheca, whose apertures open on alternating sides of the stipe; these are also clearly visible at each dichotomy in isolated material. Such a pattern of thecae is strongly reminiscent of typical anisograptids, but careful examination has failed to reveal any hint of a stolon system embedded in the dorsal margin.

Thecal style is consistent throughout the rhabdosome, autothecae possessing concave ventral margins with flared apertures which occupy about one half total stipe width. Interthecal septae have an initial inclination of 10° to the dorsal margin, increasing ventrally to 20–30°. Thecal overlap is approximately one half total thecal length. Thecal density is unusual in that it increases from 8 in 10 mm proximally to 10 in 10 mm distally. It is unclear whether this is due to more steeply inclined thecae, shorter thecae, or greater thecal overlap, but is opposite to the situation found in most graptolites where thecal density decreases distally.

Remarks. All previously described specimens of *A. victoriae*, including the types, have been small rhabdosomes with only second order dichotomies. However, the lectotype has identical proximal dimensions and form and we have no hesitation in assigning our material to this species.

Bulman (1941) was the first to recognize that *A. clarki* was synonymous with *A. victoriae*. Berry (1966) subsequently considered the two to be distinct taxa, *A. clarki* being distinguished by lateral rather than dichotomous branching and less strongly declined stipes. Cooper (1979a) remarked that the two would probably prove conspecific; Cooper and Stewart (1979) formally synonymized them.

EXPLANATION OF PLATE 4

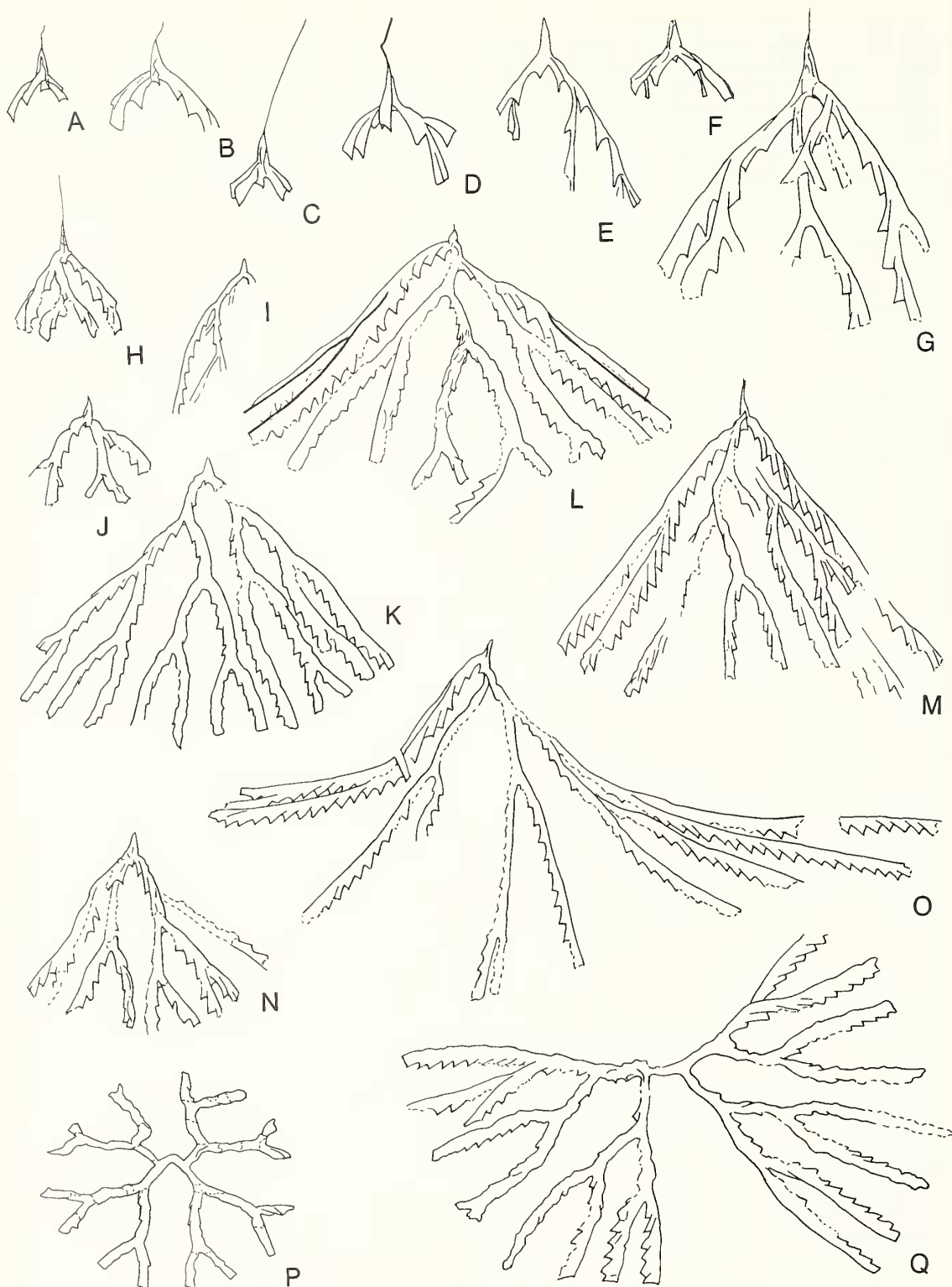
Figs 1–8. *Paratemnograptus isolatus* gen. et sp. nov. 1, GSC 87449, SPI43. 2, GSC 87450, SPI43. 3, GSC 87439, MPS42C. 4, GSC 87482, MPS42C. 5, GSC 87424, MPS42C. 6, GSC 87435, MPS42C. 7, GSC 87486, MPS42C. 8, GSC 87440, MPS42C. All ×40.

Figs 9–14. *Aorograptus victoriae* (T. S. Hall, 1899). 9 and 11, GSC 87437, MPS42C, ×20. 10, GSC 87418, note bitheca, MPS42C, ×20. 12, GSC 87422, MPS42C, ×20. 13, GSC 87477, MPS42C, ×40. 14, GSC 87425, MPS42C, ×40.

Scanning electron micrographs of isolated specimens.



WILLIAMS and STEVENS, *Paratenmograptus*, *Aorograptus*



TEXT-FIG. 11. For legend see opposite.

We see no justification in retaining two separate species in the light of our own work and that of previous authors, and therefore follow Bulman (1941) and Cooper and Stewart (1979) in regarding *A. clarki* as a junior synonym of *A. victoriae*.

The species of '*Bryograptus*' figured by Hall (1914) and Bulman and Cooper (1969) is identical to our mature specimens of *A. victoriae*. Specimens assigned to '*B. pauxillus*, sp. nov.' (Benson 1933) and '*B. hunnebergensis* Moberg' (Benson and Keble 1936) were recognized by Bulman (1941, p. 115) as belonging to *A. victoriae*. The proximal ends of '*Bryograptus simplex* Törnquist' figured by Benson and Keble (1936) appear similar in branching pattern and overall form to *A. victoriae*, but the sicula is much longer (3 mm and 4.5 mm if their magnifications are correct). Törnquist's original specimens (1904, pp. 3–4, pl. 1, figs 1–4) have a similarly long sicula, but are recorded from the *T. phyllograptoides* Zone of southern Sweden. Williams and Stevens (1988a) considered this interval to be equivalent to the lower Arenig *T. akzharensis* Zone of the Cow Head Group. It is therefore most likely that *B. simplex* is synonymous with *Pendeograptus fruticosus* (J. Hall) or *P. cf. P. pendens* (Elles) as described by Williams and Stevens. The similarity of *A. victoriae* to the lower Arenig *P. fruticosus* is remarkable: proximal development, rhabdosome branching and thecal style (autothecae in *A. victoriae*) are all very similar, although the two may be distinguished by the longer sicula of *P. fruticosus* and bithecae and more numerous branching in *A. victoriae*.

The various Chinese and Russian species described by Mu (1955), Wang *et al.* (1979) and Tzaj (1968, 1974) all appear to be synonymous with *A. victoriae*, as do the specimens figured by Wang *et al.* (1979, fig. 9a) as *A. simplex* (Törnquist).

As noted in the discussion of *Aorograptus*, the original assignation of *A. victoriae* to *Bryograptus* is invalid following the definition given by Bulman (1970, p. V39), who stated that *Bryograptus* is an anisograptid which develops 'from three primary stipes by irregular and apparently lateral branching'. Obut's (1957) inclusion of both *Bryograptus* and the dichograptid genus *Pendeograptus* within a family Bryograptidae is therefore clearly unacceptable.

Genus ADELOGRAPTUS Bulman, 1941

Type species (by original designation). *Bryograptus*? *Hunnebergensis* Moberg, 1892, p. 92, pl. 2, figs 5–7 (?8 and 9).

Diagnosis. (revised using Bulman 1941, p. 114). Rhabdosome declined or horizontal, often somewhat lax and flexuous, formed from two primary branches by regular or irregular, commonly delayed, dichotomous branching. Sicular bitheca always present, additional bithecae and stolothecae present in some species, absent in others, autothecae straight, with simple apertures and low inclination, stipes consequently slender.

Remarks. The revision of *Adelograptus* permits incorporation of many slender, regularly branching taxa previously accommodated within the rather unsatisfactory genus *Clonograptus*. The type species of *Clonograptus* (*C. rigidus*) is now recognized as having a Lower Arenig age and probably belongs within the dichograptids (see previous discussion in text). Other more robust, pendent species originally assigned to *Bryograptus* (e.g. '*B. victoriae*') but since transferred to *Adelograptus* (Bulman 1941) because of their two primary stipes are here assigned to a new genus *Aorograptus* (see generic remarks).

Although such a classification still has its limitations, it is closer to a true phylogenetic grouping

TEXT-FIG. 11. *Aorograptus victoriae* (T. S. Hall, 1899), A–G $\times 5$, H–Q $\times 2.5$. A, GSC 87374, GP38. B, GSC 87401, GP38. C, GSC 87405, GP38. D, GSC 87297, CHN8.32. E, GSC 87295, CHN8.34. F, GSC 87367, GP38. G, GSC 87397, GP38. H, GSC 87326, MPS42C. I, GSC 87379, GP38. J, GSC 87332, MPS42C. K, GSC 87310, MPS42C. L, GSC 87309, MPS42C (also figured Pl. 2, fig. 1). M, GSC 87355, MPS42C. N, GSC 87321, MPS42C. O, GSC 87320, MPS42C. P, GSC 87336, MPS42C. Q, GSC 87313, MPS42C.

than that used previously, all members having similar proximal developments and thecal styles. It permits the transfer of *Clonograptus tenellus* Linnarsson to *Adelograptus* as suggested by Maletz and Erdtmann (1987), making sense of Hutt's (1974) observation that *C. tenellus* and *A. lumnebergensis* have identical proximal development patterns and may only be distinguished following subsequent branching.

In his original diagnosis, Bulman (1941) stated that branching in *Adelograptus* was apparently lateral rather than dichotomous. All studies using isolated material of the genus since that time, including the present study and that of Hutt (1974), have found branching to be dichotomous; the diagnosis is therefore consequently emended.

The genus *Paradelograptus* was erected recently by Erdtmann *et al.* (1987) for non-bithecate forms which would previously have been assigned to *Adelograptus* or *Clonograptus*. The genus is characterized by slender thecae with simple or modified apertures, and considered to be ancestral to *Kinnegraptus* Skoglund, 1961 and other kinnegraptid genera. All their described species are from the lower Arenig and lack a sicular bitheca; none of our taxa may therefore be accommodated within this genus.

Adelograptus altus sp. nov.

Plate 5, figs 9–13; Plate 5, figs 14? and 15?; Text-fig. 12A–G

1979 *Adelograptus* sp.; Cooper and Stewart, text-fig. 7d–f, h (no description).

Derivation of name. From *altus* (Latin) meaning 'high', in reference to the relatively high level of divergence of the first two thecae from the sicula.

Type specimen. The holotype is GSC 87430, an isolated specimen mounted on an SEM stub, from MPS42C. Figured Plate 5, figure 12.

Diagnosis. Sicula 1.5–1.8 mm long with distal convex curvature, with both rutellar and antirutellar margins free distally. Sicular bitheca opens at same level where ventral wall of $th1^1$ diverges from sicula. $Th1^1$ and 1^2 are gently declined with concave free ventral margins and gently flared apertures, increasing from 0.2 mm diameter to 0.4–0.5 mm at the aperture.

Material and localities. Nine isolated, three-dimensional proximal fragments, eight flattened, non-isolated proximal fragments. Several possible mature, non-isolated rhabdosomes. From CHN8.30, SPI43, MPN17B, MPS42C.

Description. The species is defined primarily on its distinctive pattern of proximal development. Overall form is apparently similar to that of *A. cf. tenellus* (Moberg) with the exception of a slightly narrower funicle, but the two are clearly separated by the proximal form seen both in flattened and isolated material.

The sicula is 1.5–1.8 mm long measured along the rutellar margin, with a distal convex curvature. The sicular aperture is 0.2–0.25 mm wide, with a pronounced rutellum extending 0.05–0.1 mm beyond the antirutellar margin. $Th1^1$ buds from the prosicula on the rutellar side, growing down along this margin for 0.6–0.75 mm

EXPLANATION OF PLATE 5

Figs 1–8. *Aorograptus victoriae* (T. S. Hall, 1899). 1, GSC 87421, MPS42C, $\times 40$. 2, GSC 87457, MPS42C, $\times 40$. 3, GSC 87426, MPS42C, $\times 40$. 4, GSC 87475, $\times 40$. 5, GSC 87472, MPS42C, $\times 20$. 6, GSC 87453, MPS42C, $\times 40$. 7, GSC 87478, MPS42C, $\times 20$. 8, GSC 87487, MPS42C, $\times 20$.

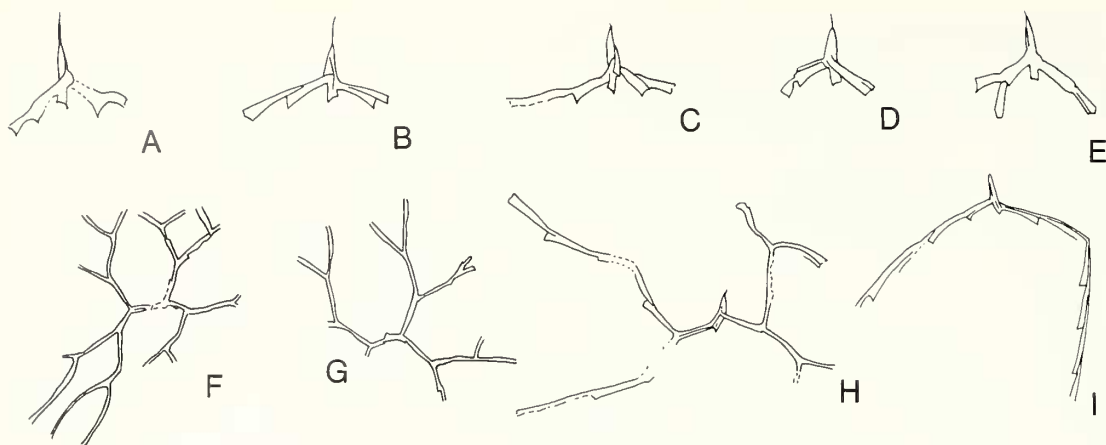
Figs 9–13. *Adelograptus altus* sp. nov. MPS42C, $\times 40$ except Fig. 11 ($= \times 20$). 9, GSC 87429. 10 and 11, GSC 87441. 12, GSC 87430, Holotype. 13, GSC 87455.

Figs 14 and 15. *Adelograptus altus* sp. nov.? Juvenile growth stages, $\times 40$. 14, GSC 87460, GP38. 15, GSC 87427, MPS42C.

Scanning electron micrographs of isolated specimens.



WILLIAMS and STEVENS, *Aorograptus*, *Adelograptus*



TEXT-FIG. 12. A–G, *Adelograptus altus* sp. nov., A–E $\times 5$, F and G, $\times 2.5$. A, GSC 87302, MPN17B. B, GSC 87377, GP38. C, GSC 87360, MPS42C. D, GSC 87337, MPS42C. E, GSC 87341, MPS42C. F, GSC 87285, CHN8.30. G, GSC 87300, SPI43. H and I, *Adelograptus antiquus* (T. S. Hall, 1899)?, $\times 5$. H, GSC 87340, MPS42C. I, GSC 87416, GP40.

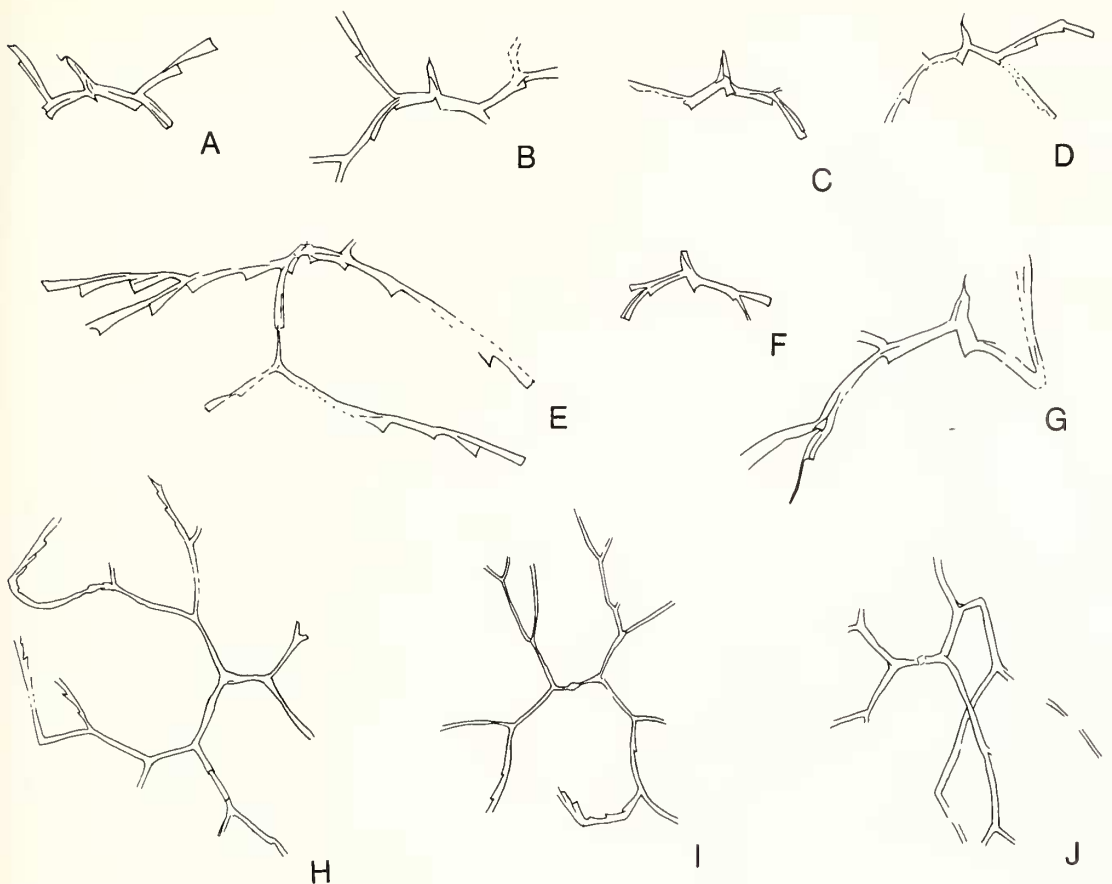
before turning sharply out, subtending an angle of $70-80^\circ$ with the distal sicular axis. The rutellar wall of the sicula is free for 0.4–0.6 mm distally, while the sicular bitheca opens cryptically at the same level at which the ventral wall of $th1^1$ diverges from the sicula. The point of origin of the bitheca is unclear and appears to be concealed by the early dorsal wall of $th1^1$. The stipe is 0.15–0.2 mm wide where $th1^1$ leaves the sicula; the free ventral wall of $th1^1$ has as strong concave curvature, leading to a splayed-out aperture and an undeformed apertural stipe width of 0.4–0.5 mm. The ventral wall of $th1^1$ is free for 1.0–1.2 mm before the aperture is reached, which is 0.25–0.3 mm wide (i.e. two-thirds of total stipe width).

$th1^2$ buds from $th1^1$ 0.5 mm below its origin, growing immediately across and down the sicula at $45-50^\circ$ from the sicular axis. Development may be either right- or left-handed; it is therefore meaningless to discuss reverse and obverse aspects of the sicula, as these vary from one specimen to the next. Once $th1^2$ has reached the antirutellar margin of the sicula it turns up slightly, subtending an angle of $30-40^\circ$ with the distal sicular axis in most cases. It has a similar concave ventral margin and splayed-out aperture to $th1^1$, the stipe width measuring 0.2 mm initially, but increasing to 0.4–0.5 mm (undeformed) by the aperture.

The budding of $th2^1$ and 2^2 appears to be typically isograptid, with $th1^2$ dicalycal. There is no evidence for further dichotomies in isolated material, but one non-isolated specimen assigned to this species (Text-fig. 12E) and those of Cooper and Stewart (1979) show dichotomous branching of $th2^1$ and 2^2 . Measurement of several slender 'clonograptid' rhabdosomes demonstrates several with funicles of equivalent width to that which would be expected from isolated specimens. We conclude that although branching is variable, mature rhabdosomes have overall appearances of those specimens illustrated in Text-figure 12F, G.

Remarks. The description of *A. altus* is based primarily on isolated, three-dimensional material, making comparison with other similar *Adelograptus* species difficult if known only from flattened, non-isolated specimens. The proximal budding pattern is similar to those shown by *A. cf. A. tenellus* and *Adelograptus* sp. A, but the sicula is longer than that of *A. cf. A. tenellus* and shorter than that of *Adelograptus* sp. A, while most specimens have a prominent 'notch' between the free ventral wall of $th1^2$ and the distal antirutellar margin of the sicula. Comparison using overlays clearly shows the incompatibility of the three species in terms of exact budding patterns and angles of thecal inclination.

The specimens figured by Cooper and Stewart (1979) as *Adelograptus* sp. are identical to those described here, with the exception of $th1^1$ which is marginally shorter. Unfortunately they did not describe their material or make any reference to it in the text. No other comparable specimens have been described or figured previously.



TEXT-FIG. 13. *Adelograptus* cf. *A. tenellus* (Linnarsson, 1871), A-F $\times 5$, G $\times 10$, H-J $\times 2.5$. A, GSC 87403, GP38. B, GSC 87389, GP38. C, GSC 87409, GP38. D, GSC 87303, MPN17B. E, GSC 87347, MPS42C. F, GSC 87348, MPS42C. G, GSC 87349, MPS42C. H, GSC 87398, GP38. I, GSC 87394, GP38. J, GSC 87395, GP38.

Adelograptus cf. *A. tenellus* (Linnarsson, 1871)

Plate 2, figs 2 and 3; Text-fig. 13A-J

cf. 1871 *Dichograptus tenellus*; Linnarsson, p. 795, pl. 16, figs 13-15.

cf. 1909 *Clonograptus tenellus* Linnarsson (and vars.); Westergård, pp. 68-72, pl. 4, figs 17-29.

cf. 1929 *Clonograptus tenellus* (Linnarsson); Stubblefield, pp. 278-262, text-figs 1, 8-11.

1936 *Bryograptus hunnebergensis* Moberg; Benson and Keble (*pars*), pp. 269-270, pl. 30, figs 14 and 15 (non pl. 30, figs 1-11 = *A. victoriae* (T. S. Hall)).

cf. 1987 *Adelograptus tenellus* (Linnarsson); Maletz and Erdtmann, pp. 180-182, pl. 1, figs a-c; pl. 2, figs a-m.

Material and localities. About ten flattened specimens from MPN17B, MPS42C and GP38 and five isolated, three-dimensional specimens from MPS42C.

Description. Rhabdosome with several slender stipes formed by delayed dichotomous branching from two primary stipes. The largest rhabdosome seen has a diameter of about 30 mm, with four dichotomies on the most complete portion, suggesting a total of thirty-two stipes. Dichotomous branching is apparently irregular, with a normal spacing of 3-5 mm (i.e. every two or three thecae). Thecal outline is rarely seen owing to

preservation in scalariform view, but when present stipe width is seen to measure 0.35–0.4 mm proximally, increasing distally to a maximum 0.6 mm.

The sicula is 1.1–1.4 mm long, and has a gentle convex curvature with respect to the rutellar margin in the distal one-third to one half its length. It is 0.2–0.25 mm wide at the aperture, with a slight rutellum. Th1¹ buds from the prosicula on the rutellar margin. It grows down in contact with this margin for 0.6–0.7 mm, before deflecting sharply out, subtending an angle of about 100° with the sicular axis. This leaves the distal rutellar margin of the sicula free for 0.4–0.5 mm. Th1¹ then curves gently downwards until its aperture is reached, leaving a free ventral wall 1.0–1.1 mm long. The thecal aperture is 0.3 mm wide with a prominent flaring at the tip in some specimens. A sicular bitheca is present, originating a little below the point of origin of th1¹ on the obverse side. The level of its aperture lies a little above the point of deflection of th1¹, and is therefore not seen except in isolated specimens.

Th1² buds high up from th1¹, growing down and across the sicula on the reverse side, then curving out so that its ventral wall cuts the base of the antirutellar sicular margin. It subtends an angle of 60–70° with the sicular axis at its point of divergence; this angle is maintained for the remaining 1.0–1.1 mm of growth, although the theca sometimes curves down very slightly before the aperture. The funicle formed by the sicula and first two thecae measure 2.5–2.8 mm long when preserved horizontally to bedding.

Th2^{1a} buds from th1² on the rutellar margin of the reverse side some 0.7 mm above the base of the rutellum. It follows the dorsal wall of th1¹ until just before the aperture is reached; at this point th2^{1b} buds from th2^{1a}, the two growing in contact for about 0.15 mm before the aperture of th1¹ is reached. They then diverge to give the first dichotomous branch. Although bithecae are apparently lacking on most thecae, branching fragments belonging to this or a related species show a bithecal aperture above the aperture of the autotheca when dichotomous branching occurs. Bithecae also occur at the dichotomies of several other unrelated late Tremadoc taxa, and are thought to represent an intermediate stage towards total loss of bithecae.

Th2^{2a} buds from th1² near its point of divergence from the sicula, developing and branching in a similar fashion to th2^{1a}. Each stipe then divides dichotomously every two to three thecae. Thecal density is a low, 6–7 in 10 mm where visible, although this is difficult to determine owing to frequent branching and usual preservation in scalariform view.

Remarks. *Adelograptus tenellus* was revised recently by Maletz and Erdtmann (1987), who selected a neotype and thoroughly discussed the morphological variation found within the species. They conclude the nominate species to be a lower Tremadoc form occurring definitely only in Scandinavia, the Baltic region and Britain. Records of the species from late Tremadoc strata are, therefore, likely to be erroneous. Our material differs from the type material in having a shorter funicle and noticeably lower thecal density. Variation is so great that definition of a new taxon is withheld pending further, more detailed quantitative studies of late Tremadoc material both from western Newfoundland and elsewhere.

A few previously published descriptions include material comparable to ours; some of Westergård's (1909) specimens of *C. tenellus* and varieties are very similar, but there is a great deal of variation in his figured specimens and probably more than one species represented. *C. tenellus kingi* Benson and Keble, 1936 is similar in overall form, but thecal density is extremely high (17–21 in 10 mm). Their specimen of '*C. tenellus*' (1936, pl. 32, fig. 4) also has a high thecal count. Benson and Keble (1936, pl. 30, figs 14 and 15) figured two proximal fragments more-or-less identical to our material; these are referred to *Bryograptus simplex* Törnquist in the plate description, as are figs 12 and 13. The latter two specimens have a very different appearance, are referred to '*B. hunnebergensis*' in the text, and probably belong to *A. victoriae* (see discussion of *A. victoriae* elsewhere in this paper).

The Newfoundland specimens of *A. cf. tenellus* have a wider funicle than '*C. tenellus sensu lato*' of Cooper (1979b, fig. 5c) and Cooper and Stewart (1979, fig. 8m); both these appear to be a different species.

Adelograptus antiquus (T. S. Hall, 1899)?

Text-fig. 12H, I

?1899 *Leptograptus antiquus*, n. sp.; T. S. Hall, p. 166, pl. 17, figs 5 and 6.?1979a *Adelograptus? antiquus* (T. S. Hall); Cooper, pp. 51–54, pl. 2, fig. c–e; fig. 17a–k, 18.?1979 *Kiaerograptus antiquus* (T. S. Hall); Cooper and Stewart, pp. 791–792, text-fig. 8d, e. (summary only)*Material and localities.* Two flattened specimens from MPS42C and GP40.*Remarks.* Careful comparison of these two specimens with *Adelograptus* species from western Newfoundland reveals them to differ in terms of their small, slender sicula, wide funicle and low thecal density. These however appear to agree with those given for *A. antiquus* by Cooper (1979a) in his detailed revision of the species, but are insufficient for certain identification. Their slender, widely spaced proximal region is reminiscent more of *Adelograptus* than *Kiaerograptus*, which is why we return the species to the former genus as assigned questionably by Cooper (1979a).*Adelograptus* sp. A

Plate 6, figs 1–5; Text-fig. 14H, J

Material and localities. Three flattened, non-isolated specimens from MPN17B, MPS42C and GP40. Nine three-dimensional, isolated specimens from MPS42C.*Description.* This species is known only from isolated and non-isolated proximal fragments; overall form of the rhabdosome is consequently uncertain.

The most distinctive feature is the long, thin sicula, which is commonly 1.5 mm long. It is straight throughout the first two-thirds of its length, but displays a gentle, distal convex curvature with respect to the rutellar margin. The rutellum is pronounced, extending 0.15–0.2 mm beyond the antirutellar margin.

Th1¹ buds from the prosicula, growing down along the rutellar margin for 0.6–0.8 mm before bending out sharply, subtending an angle of 60–70° with the sicular axis and leaving the rutellar margin free for 0.5–0.6 mm. A prominent sicular bitheca buds from the sicula about half way down the metasacula on the reverse side. It has a prominent aperture lying between the rutellar margin of the sicula and ventral wall of th1¹, a little below the point where the ventral wall of th1¹ leaves the sicular margin. Th1¹ is 0.2 mm wide at the point where it diverges from the sicula. Its free ventral wall is 0.9–1.1 mm long and almost straight, but flares towards the aperture which measures 0.4 mm wide (one half total stipe width).Th1² buds from th1¹ on the obverse side just above its point of deflection. It grows down and across the sicula, the ventral wall diverging from the antirutellar margin a little above the sicular aperture. This occasionally results in a slight 'notch' at the base of the antirutellar wall. Th1² grows down at 40–50° from the distal sicular axis; it is almost straight but flares slightly towards the aperture. The free ventral wall is 0.7–0.8 mm (i.e. less than that of th1¹), while thecal widths are similar.Development of th2¹ and th2² is as found for other associated taxa; one or both are sometimes dichotomous, or dichotomies may be delayed by one or more thecae. As stated above, overall form of the rhabdosome is uncertain.*Remarks.* This species may be distinguished from other coexisting taxa by its long, slender sicula and levels of divergence of th1¹ and th1² from the sicula. Dichotomous branching is irregular and may be delayed or consecutive. As the overall form of the rhabdosome is uncertain and only limited material is available, it would be unwise to formally erect a new species at the present time.No previously described taxa of similar type have a sicula approaching this size. From the few larger fragments found, overall style of branching appears to be most similar to the irregular form of *Adelograptus antiquus* (T. S. Hall).

Adelograptus filiformis sp. nov.

Text-fig. 14A-G

?1936 *Bryograptus* (?) *antiquus* var. *inusitatus* var. nov.; Benson and Keble, pp. 267-268, pl. 30, figs 17 and 18.

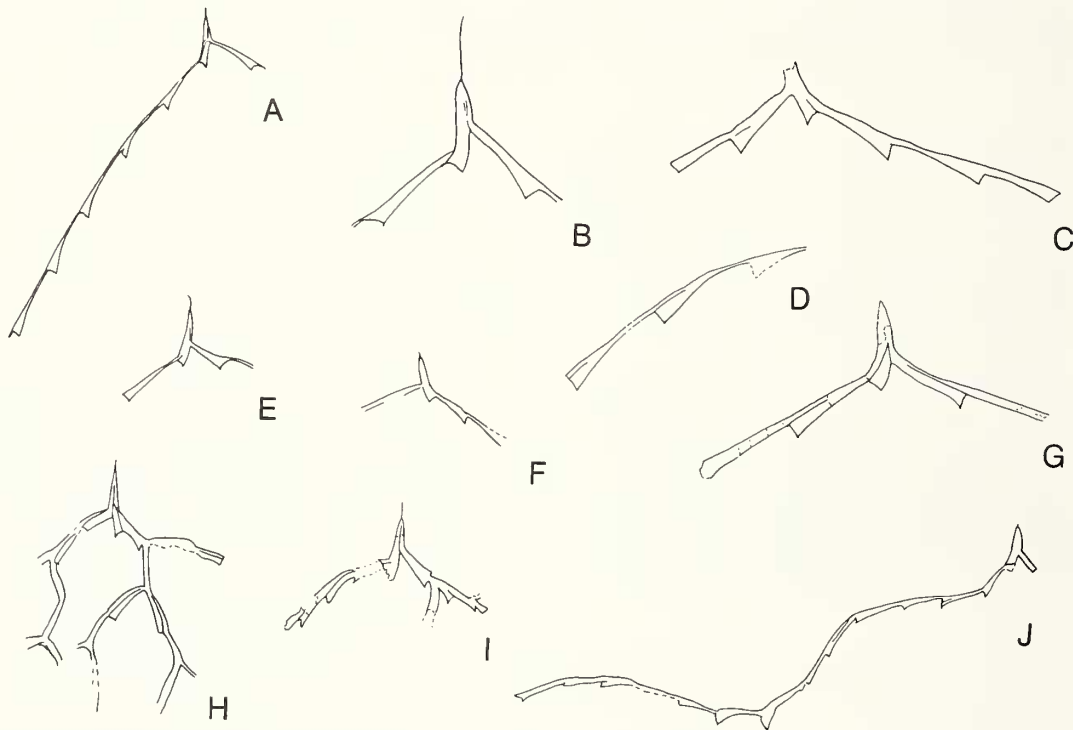
1974 *Kiaerograptus* (?) cf. *pritchardi* (T. S. Hall); Jackson, p. 51, pl. 5, fig. 3; text-fig. 2a, c, d.

?1982 *Kiaerograptus antiquus* (T. S. Hall); Gutierrez Marco, fig. 2a-e.

Derivation of name. From *filum* (Latin), meaning thread-like, in reference to the extremely slender stipes.

Type specimen. The holotype is GSC 87391, figured Text-figure 14A. From GP38.

Diagnosis. Extremely slender, biramous, declined to pendent rhabdosome, stipes measuring



TEXT-FIG. 14. A-G, *Adelograptus filiformis* sp. nov. A, GSC 87391, Holotype, GP38, $\times 5$. B, GSC 87387, GP38, $\times 10$. C, GSC 87350, MPS42C, $\times 10$. D, GSC 87298, CHN8.32, $\times 10$. E, GSC 87299, SPI43, $\times 5$. F, GSC 87304, MPN17B, $\times 5$. G, GSC 87305, MPN17B, $\times 10$. H-J, *Adelograptus* sp. A, $\times 5$. H, GSC 87417, GP40. I, GSC 87306, MPN17B. J, GSC 87312, MPS42C

EXPLANATION OF PLATE 6

Figs 1-5. *Adelograptus* sp. A. MPS42C, $\times 40$. 1, GSC 87469. 2, GSC 87431. 3, GSC 87484. 4 and 5, GSC 87468. Figs 6-10. Stipe fragments and branches from indet. *Adelograptus*. MPS42C. 6 and 7, GSC 87438, $\times 20$. 8, GSC 87432, $\times 40$. 9, GSC 87466, $\times 20$. 10, GSC 87485, $\times 40$. Figs 11-15. Indet. juvenile growth stages. 11, GSC 87445, SPI43, $\times 40$. 12, GSC 87489, SPI43, $\times 40$. 13, GSC 87447, SPI43, $\times 40$. 14, GSC 87463, GP38, $\times 80$. 15, GSC 87461, GP38, $\times 80$. Figs 16-18. *Clonograptus* sp. B. 16, GSC 87458, MPS42C, $\times 40$. 17, GSC 87428, MPS42C, $\times 20$. 18, GSC 87467, MPS42C, $\times 20$.

Scanning electron micrographs of isolated specimens.



WILLIAMS and STEVENS. *Adelograptus*, *Clonograptus*

0.2–0.3 mm at thecal apertures, but only 0.08–0.1 mm directly after apertures. Sicula with bitheca, other bithecae apparently lacking. $th1^1$ with high divergence, leaving 0.5–0.6 mm of distal sicula wall free. Thecal density 6–6.5 in 10 mm.

Material and localities. Two probable isolated fragments from MPS42C. Eleven non-isolated, flattened specimens from CHN8.32; SPI43; MPN17B, MPS42C; GP38.

Description. The rhabdosome consists of two extremely slender, gently declined stipes. The longest stipes fragment present in the material from western Newfoundland is only 10 mm long; one of the specimens figured by Jackson (1974, text-fig. 2d) however had stipe about 18 mm long with strong convex curvature, such that distally the stipes pointed inwards. Stipe width at the initial free part of each theca is a uniform 0.08–0.1 mm, increasing to 0.2–0.3 at the aperture.

The sicula is 1.2–1.4 mm long, with an apertural width of 0.2–0.25 mm. It is inclined with respect to the stipes, has a strong convex curvature with respect to the rutellar margin and a pronounced rutellum. Proximal development is unclear; $th1^1$ buds from the prosicula and grows down in contact with the rutellar wall of the sicula for only about 0.5 mm before diverging sharply out, subtending an angle of 60–70° with the sicular axis. The distal rutellar margin of the sicula is left free for 0.5–0.6 mm (rarely 0.4 mm). The dorsal thecal margin remains straight, but the ventral wall curves gently down towards the aperture, such that inclination of the ventral wall with the dorsal stipe margin increases from about 0° proximally to 30° at the level of the aperture. The free portion of $th1^1$ is of variable length, measuring 1.2–1.5 mm (cf. Jackson 1974, whose specimens had an extremely short free portion of 0.5–0.8 mm). The aperture of $th1^1$ and remaining thecae occupies two thirds of total stipe width. Although no hint of a sicular bitheca has been seen in any flattened, non-isolated specimens, the isolated material clearly shows a small bithecal aperture in the notch left by the divergence of $th1^1$ from the rutellar wall of the sicula.

$th2^1$ apparently buds from $th1^1$ at its point of deflection. Initially it grows across and slightly down, then runs in contact with the antirutellar margin of the sicula until the sicular aperture is reached. It subsequently turns out at an angle of 20–30° from the distal sicular axis. The free ventral wall of $th1^1$ part of $th2^1$ and that of all subsequent thecae behave as $th1^1$. The origin of $th2^1$ is unclear; if development is similar to other species from this assemblage, it would bud from $th1^2$. In this instance, it must have an extremely slender protheca less than 0.05 mm wide. With the exception of the sicular bitheca, there appears to be no other bithecae in the rhabdosome, neither does there appear to be any branching. Thecal density is exceptionally low throughout the rhabdosome, at a constant 6–6.5 in 10 mm.

Remarks. The only previous certain record of this distinctive but elusive species was by Jackson (1974), who referred it to *K.?* cf. *pritchardi*. His specimens from the Yukon, northern Canada are very similar but differ in the shorter free portion of $th1^2$ (0.5–0.8 mm as opposed to 1.2–1.5 mm). The free portion of $th1^2$ is, however, comparable in length to that of our specimens (1.3–1.7 mm as opposed to 1.2–1.4 mm), as is thecal density and stipe width. Judging from his illustrated examples, it appears that such variation may have been due to tectonic stretching (note particularly his text-fig. 2d).

Although several other slender taxa found within this stratigraphical interval are similar in appearance, *K. filiformis* may be reliably distinguished from them all by its high divergence of $th1^1$ from the sicula, extremely narrow stipes in the portion immediately following the apertures, and low thecal density. As recorded by Jackson (1974), no specimen seems to have possessed more than two stipes.

Cooper (1979a) expanded the definition of *Adelograptus antiquus* (T. S. Hall) to include a variety of forms with siculae and first two thecae of varying dimensions and emphasizing the symmetry of the proximal end. We accept this revision, but our specimens fall well outside his described population with a consistently longer and more slender sicula and longer first two thecae. Thecal spacing is also lower at 6–6.5 in 10 mm instead of 7 in 10 mm. Some of Cooper's end members (e.g. Cooper 1979a, fig. 17h) approach *A. filiformis*, but are still noticeably different. Cooper (1979a) included *K.?* cf. *pritchardi* of Jackson (1974) and *B.?* *antiquus inusitatus* Benson and Keble, 1936 with *A. antiquus*. Although they appear to be tectonically deformed, in our opinion Jackson's specimens seem closer to *A. filiformis* than to *A. antiquus*, with the exception of a short $th1^1$.

Although Jackson (1974) recorded thecal density as 9–10 in 10 mm, this varies from 7–10 in 10 mm in his figured specimens, depending on orientation to stretching direction. Cooper (1979*a*, p. 53) pointed out that Benson and Keble's figured specimen of *B.?* *antiquus inusitatus* differed from their written description, notably by having wider thecal spacing (3–3·5 instead of 6–7 in 10 mm). This would seem to be caused by an error in scale of illustration (probably $\times 4$ rather than $\times 2$), but as their types have not been located (Cooper, 1979*a*, p. 33), this is impossible to ratify, neither is the affinity of *B.?* *antiquus inusitatus* with either *A. antiquus* or *A. filiformis*.

Genus CLONOGRAPTUS Nicholson, 1873

Type species. *Graptolithus rigidus* J. Hall, 1858, p. 146. Subsequently designated by Miller (1889, p. 179).

Remarks. *Clonograptus* has been considered a typically 'dendroid' genus (in the traditional sense: cf. Fortey and Cooper 1986) by most authors since its original designation, although the dichograptid appearance of its autothecae and apparent lack of bithecae or stolon system has been noted by several workers (e.g. Jackson 1973; Braithwaite 1976). Recognizing this, Maletz and Erdtmann (1987, p. 180) included *Clonograptus* within the Dichograptidae rather than the Anisograptidae, and transferred many taxa previously included within the genus to *Adelograptus*.

We consider the type species of *Clonograptus* to be synonymous with one of Hall's other species, '*Graptolithus*' (usually referred to *Clonograptus*) *flexilis*, first described in the same publication as *C. rigidus* on the preceding page (J. Hall 1858, pp. 145–146). It could be argued that *C. rigidus* is therefore a junior synonym of *C. flexilis*, but we consider it best to retain *C. rigidus* as the species name in the cause of nomenclatorial stability.

Restudy of Hall's type material from Levis, Quebec by one of us (S.H.W.), revealed the types of both species to originate from the lower Arenig of that locality, an interval equivalent to the *T. akzharensis* Zone of western Newfoundland (Williams and Stevens 1988). This zone separates the *T. approximatus* Zone from the overlying *P. fruticosus* Zone. In both regions, diverse assemblages of both dichograptids (e.g. *Tetragraptus*, *Didymograptus* (*Expansograptus*), *Pendeograptus*, *Pseudophyllograptus*) and traditional 'dendroid' taxa (e.g. *Rhabdinopora*, *Dendrograptus*, *Arcanthograptus*) are present. Although three-dimensional, isolated material was not recovered from this interval, the representatives of *Clonograptus* do indeed appear to bear more resemblance to the dichograptids than to the anisograptids, and we tend to agree with the conclusions of Maletz and Erdtmann (1987). Erdtmann *et al.* (1987, p. 123) transferred *Clonograptus smithi* Harris and Thomas, 1938 to their new kinnegraptid genus *Paradelograptus*. *C. smithi* is, however, from the lower Bendigonian (equivalent to the *T. approximatus* or *T. akzharensis* zones) and appears very similar to *C. rigidus*/*C. flexilis*.

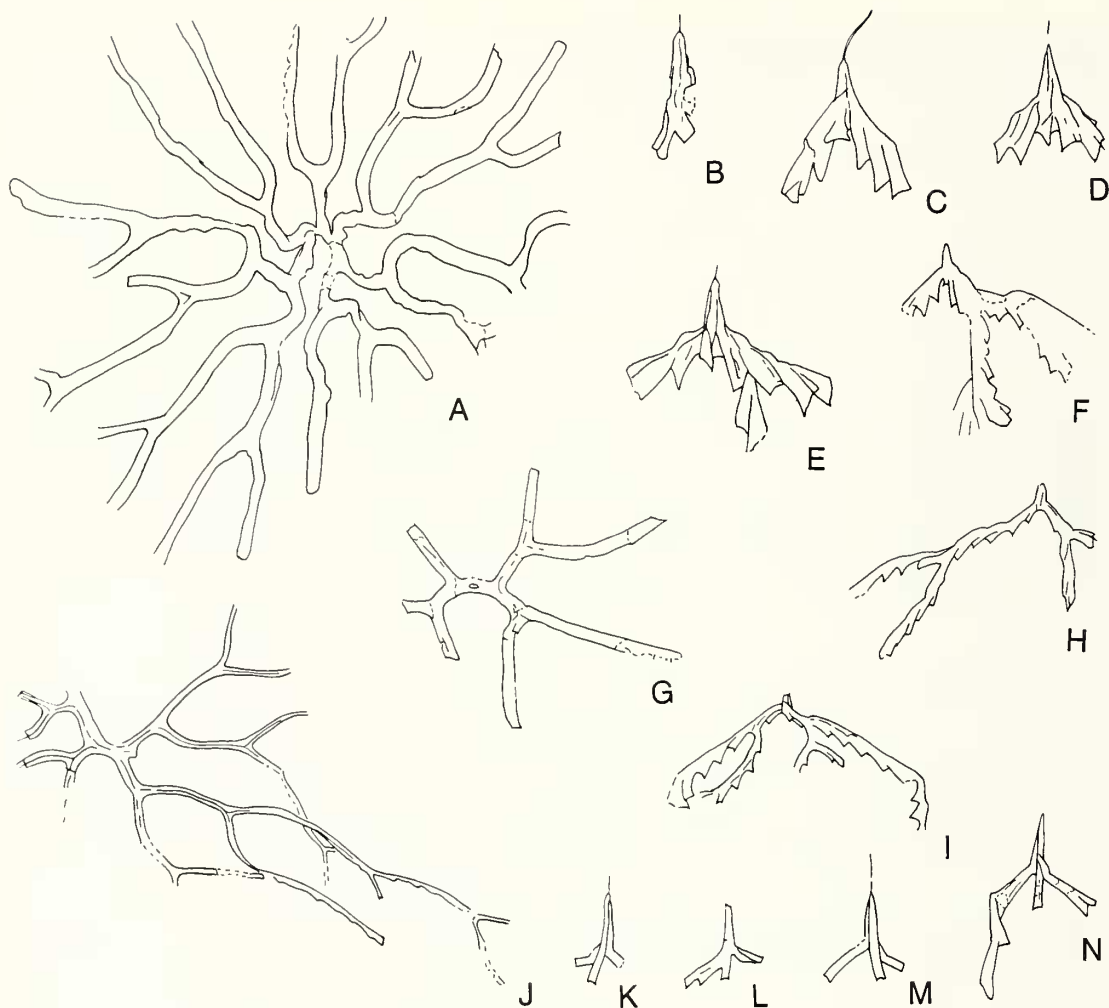
If typical *Clonograptus* belongs to the Dichograptidae, it is unlikely that taxa from the lower, middle or even upper Tremadoc should be assigned to the genus if the presence of bithecae or a stolon system is considered of taxonomic significance at the generic level. Final revision of the generic definition should, however, be withheld until isolated material of '*Clonograptus*' has been recovered from both the Tremadoc and lower Arenig. We therefore here refer our late Tremadoc '*Clonograptus*-like' taxa to '*Clonograptus*?'.

Clonograptus? sp. A.

Plate 2, fig. 6; Plate 6, figs 16–18; Plate 7, figs 1–5; Text-fig. 15A–F

Material. Several flattened specimens from CHN8.32, MPS42C and GP38. Ten isolated, three-dimensional specimens from MPS42C.

Description. The rhabdosome reaches over 30 mm in diameter, somewhat irregular, delayed dichotomous branching producing up to at least thirty-two stipes distally from the two primary stipes. The proximal region



TEXT-FIG. 15. A–F, *Clonograptus* sp. A, A and F $\times 2.5$, B–E $\times 5$. A, GSC 87418, GP40. B, GSC 87342, MPS42C. C, GSC 87343, MPS42C. D, GSC 87373, GP38. E, GSC 87380, GP38. F, GSC 87344, MPS42C. G–I, *Clonograptus* sp. C, $\times 2.5$. G, GSC 87351, MPS42C. H, GSC 87346, MPS42C. I, GSC 87419, GP40. J, *Clonograptus* sp. B, GSC 87314, MPS42C, $\times 2.5$ (also figured Pl. 2, fig. 5). K–N, *Rhabdinopora* sp., MPS42C, $\times 5$. K, GSC 87338. L, GSC 87345. M, GSC 87352. N, GSC 87353.

EXPLANATION OF PLATE 7

Figs 1–5. *Clonograptus* sp. A. MPS42C, all $\times 40$ except Fig. 3 ($= \times 20$). 1, GSC 87479. 2, GSC 87481. 3, GSC 87423. 4, GSC 87470. 5, GSC 87476.

Figs 6–12. *Rhabdinopora* sp. 6, GSC 87451, SPI43. 7, GSC 87456, MPS42C. 8, GSC 87483, MPS42C. 9, GSC 87452, SPI43. 10, GSC 87419, MPS42C. 11, GSC 87454, MPS42C. 12, GSC 87420, MPS42C. All $\times 40$, except fig. 6 ($= \times 80$).

Figs 13–17. Indet. dendroid distal fragments. 13, GSC 87448, SPI43. 14 and 15, GSC 87464, GP38. 15, GSC 87471, MPS42C. 17, GC 87480, MPS42C. All $\times 40$ except fig. 17 ($\times 80$).

Scanning electron micrographs of isolated specimens.



is generally preserved in scalariform view, with stipe widths of about 0.7 mm; distal stipe widths are similar, both in scalariform and lateral aspect. The stipes have an irregular appearance owing to the presence of bithecae throughout the rhabdosome. Dichotomous branching occurs throughout the rhabdosome at intervals of 2–8 mm; failed dichotomies commonly result in asymmetrical rhabdosomes.

The sicula is about 2 mm long, with a distinctive concave apertural outline formed by a prominent rutellum and slight antirutellar process. Proximal development has not been observed clearly, but appears to be similar to most coeval graptolites, with a prominent sicular bitheca opening at the level of divergence of the ventral wall of $th1^1$ from the rutellar margin. $th1^1$ and 1^2 are strongly declined, giving a narrow, pendent appearance to the proximal region. Their free ventral margins are gently concave and are 1.8–2.0 mm long. The funicle is normally deformed due to flattening of the rhabdosome in a plane perpendicular to that of the sicula, $th1^1$ and 1^2 . Both $th1^2$ and 2^1 dichotomise, as do many subsequent thecae, giving rise to the multi-stiped rhabdosome.

All autothecae apparently possess bithecae, opening on alternate sides of the stipes. The ventral margins of autothecae display gentle concave curvature, have simple apertures occupying one half to one third total stipe width and have an almost uniform spacing of ten in 10 mm throughout the rhabdosome.

Remarks. This species appears to differ from all described previously, but inadequate material exists to justify formal erection of a new taxon. The overall appearance of the rhabdosome and thecal style is reminiscent of *Clonograptus kingi* Benson and Keble, 1935. Their species is, however, minute, with slender stipes 0.2 mm wide and a very high thecal density.

Both proximal and distal isolated fragments are extremely distinctive, owing to their robust form, ubiquitous bithecae, and curved autothecae. Although very different in proximal appearance and thecal style, it is sometimes difficult to distinguish poorly preserved specimens from *Aorograptus victoriae* preserved in dorsal view. The latter species possesses more simple autothecae, only has bithecae at dichotomies, and the proximal region has a very different appearance.

Clonograptus? sp. B.

Plate 2, fig. 5; Text-fig. 15j

Material. Two flattened specimens from MPS42C and GP38.

Remarks. These two specimens are preserved in scalariform orientation, and characterized by heavy cortical thickening in the proximal region. This reduces distally, resulting in narrowing stipes. Details of lateral stipe width, thecal style, etc., have not been observed due to both orientation of the rhabdosome and to the cortical thickening.

Examples of '*Clonograptus*' with similar appearance have been recorded several times before, both from the top Tremadoc and other stratigraphic levels. The specimen figured by T. S. Hall (1914, pl. 8, fig. 3) as '*C. tenellus callavei* Lapworth' and refigured by Bulman and Cooper (1969, fig. 5f) is probably identical. Our specimens are also similar in appearance to J. Hall's (1858) type specimens of *C. rigidus* and *C. flexilis* regarding their distinctive cortical thickening, but his material from the lower Arenig of Quebec reaches much greater dimensions and critical comparison is not possible. If the specimens from western Newfoundland are indeed similar to Hall's types, it demonstrates that they may be assigned unequivocally to *Clonograptus s.s.*

Clonograptus? sp. C

Text-fig. 15G–I

Material. Several flattened, fragmentary specimens from MPS42C and GP40.

Remarks. These specimens are characterised by a funicle of varying width due to irregular, commonly delayed, first dichotomous branching, relatively slender stipes 0.8 mm wide, and simple autothecae numbering about eight in 10 mm. The proximal region is gently declined and open, in contrast with *Clonograptus?* sp. A. No isolated material or well preserved flattened specimens have

been recovered exhibiting complete proximal development; it is possible that *Clonograptus?* sp. C is closer to *Aorograptus victoriae* than to *Clonograptus*, but the lack of flared apertures and overall appearance of the proximal region appear to be different from that genus.

Genus RHABDINOPORA Eichwald, 1855

Type species. *Gorgonia flabelliformis* Eichwald, 1840, p. 207. By subsequent designation of Erdtmann (1982)

Diagnosis. Rhabdosome conical (juvenile stages may possess reduced conicality), coni-siculate throughout all developmental stages, with or without proximal buoyancy structures; branching dichotomous, diverging from tricalycal or quadricalycal initial stolonal budding; stipes straight, subparallel to parallel, connected by transverse dissepiments, anastomosis rare; autothecae denticulate, commonly spined, bihecae normally inconspicuous (from Erdtmann 1982, pp. 128–129).

Remarks. Erdtmann's revision of *Dictyonema* and *Rhabdinopora*, restricting the former genus to rooted species, is here accepted. Our planktonic forms are therefore assigned to *Rhabdinopora*, although previously they would have been considered 'typical' *Dictyonema*.

Rhabdinopora sp.

Plate 2, figs 7–11, 13; Plate 7, figs 6–12; Text-fig. 15K–N

Material. Many three-dimensional, isolated fragments from SPI43 and MPS42C, and flattened specimens from all late Tremadoc localities in the Cow Head Group.

Remarks. The genus *Rhabdinopora* is currently under revision by Erdtmann and others. Characters of taxonomic importance are still uncertain, and we withhold full taxonomic treatment pending further revision of the genus. Three primary stipes are clearly visible in isolated material, and the slender sicula and proximal development are readily identifiable in flattened specimens. A 'flotation sac' is present on one of the specimens, while thecal style, dissepiments and net-like, parabolic rhabdosome are all characteristic of *Rhabdinopora*.

This ubiquitous form continues into the lower Arenig, where it is common in both the *T. approximatus* and *T. akzharensis* zones, but rare after that level. The disappearance of *Rhabdinopora* from the sections may be stratigraphically controlled, but in our opinion is more likely related to subtle changes in paleoecology.

miscellaneous indet. Graptoloids

Plate 2, fig. 12; Plate 7, figs 13–17

Remarks. A variety of distal stipe fragments are present in the late Tremadoc, flattened in the shale and as three-dimensional isolated fragments from dissolved limestone. They are not identifiable without additional, more complete material, but due to their distinctive nature a selection is here figured for completeness.

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